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THE

JOURNAL OF COMPARATIVE NEUROLOGY.

THE FORE-BRAIN OF MACACUS.

By WM. WOLFE LESEM, M. A.

With Plates I and II.

The present article is the result of investigations upon the simian brain pursued by the writer during the winter of 1900 in the anatomical laboratory of Columbia University. A careful search of the bibliography of the simian brain failed to show any article dealing with the species in question. Here and there the writer came across rather poor drawings of the macaque brain but nowhere did he meet with any description thereof except in Flatau and Jacobsohn's Comparative Anatomy of the Central Nervous System of Mammals. In the Anatomical Museum of Columbia University the writer has had access to a sufficiently large number of macaque brains to render his observations fairly accurate.

Compared with the dog, Macacus presents many striking advances. A higher type of gyri and sulci, a well developed occipital lobe with a posterior cornu, a calcar avis, a prominent forceps major, and an enormously developed temporo-sphenoidal lobe are some of the points which will be discussed in the ensuing pages.

Whereas in the dog the ventral aspect of the encephalic segments lies almost entirely in the same plane, the brain of Macacus presents that convexity of the pons Varolii so marked in man. The pons of Macacus differs moreover from that of the carnivores in being actually larger than the medulla. In the carnivores the crura cerebri are plainly visible upon the base of the brain as two large bundles of fibres which extend from the pons and diverge to enter the cerebral hemispheres opposite

the optic chiasma. The crura of Macacus are not visible on the base of the brain. They are entirely hidden from view by the well-developed temporo-sphenoidal and the occipital lobes. In contradistinction to dog and man Macacus presents but a single corpus albicans, which occupies a mesial position. We naturally expect to find a well-developed olfactory apparatus in dogs; and such is the case, for the olfactory bulb projects beyond the hemispheres. The olfactory lobes, the bulbs and the olfactory tracts of Macacus are greatly atrophied. Compared with the dog the orbital surface of the frontal lobe has likewise retrograded.

The Hemispheres.

The growth backward of the body of the lateral ventricle in Macacus results in the formation of a posterior cornu, and gives us an additional lobe, the occipital. The occipital lobe is merely a differentiation of the posterior part of the parietal lobe. In Macacus it is very extensive, comprising about a third of the entire hemisphere. In man the occipital lobe comprises less than a sixth of the secondary fore-brain.

The hemispheres of Macacus are in contact with one another throughout their entire extent; even the apical portion of the frontal lobes are contiguous. In the dog the frontal apices are slightly separated, and the rounded posterior extremities of the parietal lobes diverge considerably to permit of the reception of the worm of the cerebellum between them. The entire hemisphere of Macacus is slightly curved from before backwards. This is most marked in the frontal lobe, where the apex curves sharply downwards in a hook-like manner. This curve is due to the non-development of the orbital surface. Externally the frontal lobes are flattened. The parietal and the occipital lobes are curved only slightly.

The arrangement of the fissures and the convolutions of Macacus closely resembles the condition met with in the human foetus. The numerous annectent gyri of the adult human brain renders it difficult to homologize the gyri of the adult brain with those of Macacus. The Sylvian, the Rolandic, the

inferior occipital, the par-occipital, the calloso-marginal, and the calcarine fissures divide the hemispheres of Macacus into frontal, parietal, occipital, and limbic lobes. A brief description of these fissures is therefore desirable at this juncture.

The Sylvian fissure is oblique in direction. In man it is horizontal, in carnivores almost vertical. It starts at the base of the brain, separating the orbital surface of the frontal from the temporal lobe. At first it proceeds laterally, then obliquely upwards and backwards, and finally terminates by joining the parallel fissure. In one specimen of Macacus nemestrinus under observation, the Sylvian fissure did not join the temporo-sphenoidal. Owing to the non-development of the orbital surface of the frontal lobe, the sylvian fissure in Macacus rhesus has no anterior limb. In Macacus nemestrinus, however, there exists a small rudimentary fissure occupying the position of the anterior Sylvian limb, but not continuous with the Sylvian sulcus.

The fissure of Rolando is very similar in its course to that of man. It runs from just below the great longitudinal fissure and curves sharply forwards and downwards. Before its termination, just above the mesial portion of the Sylvian fissure, the fissure of Rolando curves slightly backwards.

The par-occipital fissure runs sinuously from the great longitudinal fissure almost to the inferior margin of the hemisphere. Externally it is hidden from view by the growth forward of the occipital lobe. This growth forward of the occipital lobe results in the formation of a fissure, the "Affenspalte." This fissure, called by some the external occipital sulcus, is peculiar to Quadrumana. Upon drawing aside the "Affenspalte" we find lying in its floor two annectent gyri belonging to the par-occipital fissure. The par-occipital fissure is joined by the parallel and the intraparietal sulci.

The inferior occipital fissure extends from the posterior margin of the occipital lobe almost to the parallel fissure. It is curved forwards and upwards, and passes just below the "Affenspalte."

The calcarine fissure lies upon the mesial aspect of the

occipital lobe. It separates the temporal lobe from the occipital. At its origin it consists of two parts, an upper limb which arises from the superior margin of the occipital lobe and a shorter, lower limb which commences a little below the centre of the occipital lobe. These two limbs unite midway between the upper and the lower margins of the cerebrum. The calcarine fissure then runs at first downwards and forwards to the base of the hemisphere. It then passes forwards and slightly upwards, and terminates in the dentate fissure.

The calloso-marginal sulcus extends from the middle of the great longitudinal fissure almost to the apex of the frontal lobe. At first it curves downwards, then courses directly forwards, and finally curves upwards to terminate in the great longitudinal fissure. Before curving upwards it gives off a short inferior limb.

The Frontal Lobe.

The frontal lobe presents three surfaces, external, internal and orbital. The external surface is bounded inferiorly by the Sylvian fissure and posteriorly by Rolando. The external surface presents two fissures, the precentral and the horizontal. The precentral fissure is vertical in direction, and lies midway between the apex of the lobe and the fissure of Rolando. Superiorly it terminates by dividing into an anterior and a posterior limb.

The horizontal fissure lies a little posterior to the apex of the frontal lobe. It runs at right angles to the precentral sulcus. Posteriorly it curves slightly upwards.

The precentral and the horizontal fissures divide the frontal lobe into three convolutions. Of these the most posterior one corresponds exactly to the ascending frontal gyrus of man being bounded anteriorly by the precentral sulcus, inferiorly by Sylvius and posteriorly by Rolando. Just what the remaining two gyri are is difficult to say. BISCHOFF declares that in the gorilla and the orang Broca's convolution is but ill-developed; and according to PANSCH the third frontal convolution is absent in all other apes. If PANSCH be correct in his

theory we may homologize the upper frontal gyrus of Macacus with the first frontal of man, and the remaining lower gyrus with the second frontal.

The mesial aspect of the frontal lobe presents the marginal gyrus enclosed by the calloso-marginal fissure. The gyrus fornicatus is continuous with that portion of the frontal lobe which in man is known as the precuneus.

We have already noted the concave non-developed orbital surface of the frontal lobe.

The Parietal Lobe.

The parietal lobe has two surfaces; an external one bounded anteriorly by Rolando, inferiorly by Sylvius, and posteriorly by the "Affenspalte," and a mesial surface which is continuous with the gyrus fornicatus. The external surface presents the intra-parietal fissure. This sulcus lies between the fissure of Rolando and the external occipital sulcus. It starts a little posterior to the fissure of Rolando, and passes upwards and backwards. Then it curves upon itself, and terminates in the par-occipital sulcus. The intra-parietal fissure was originally composed of three distinct fissures, a superior, an inferior, and a horizontal parietal sulcus. This condition is still evident in the adult human brain where the three parts of the intra-parietal sulcus are separated from one another by numerous annectent gyri.

The external surface of the parietal lobe presents two gyri, a superior and an inferior parietal gyrus. The superior parietal gyrus represents the ascending parietal and the superior parietal convolutions of man. The inferior parietal gyrus may be divided into supramarginal and angular convolutions. The supramarginal is bounded anteriorly by the intra-parietal sulcus, posteriorly by the parallel fissure, and inferiorly by the fissure of Sylvius. The angular is bounded in front by the temporo-sphenoidal sulcus, below by the inferior occipital, and behind by the external occipital.

Temporo-Sphenoidal Lobe.

This lobe is very highly developed in Macacus. Its external surface presents the parallel fissure which is the most extensive sulcus of the cerebrum. It starts near the apex of the temporal lobe, and extends almost to the great longitudinal fissure; and there it joins the parieto-occipital fissure. Inferiorly it curves slightly forward; while superiorly it curves slightly backwards. The parallel fissure divides the temporal lobe into an upper and a lower gyrus. The lower gyrus is continued on to the base of the lobe. The superior convolution lies below the supramarginal gyrus. It is bounded anteriorly and above by the Sylvian fissure, and posteriorly and below by the parallel fissure. The base of the temporo-sphenoidal lobe is divided into two convolutions by the collateral fissure. This sulcus runs almost parallel with the inferior margin of the temporal lobe. It extends from within a short distance of the posterior temporal pole almost to the apex of the lobe. The collateral fissure forms the lower boundary of the hippocampal gyrus.

The Occipital Lobe.

As in man, the occipital lobe of Macacus presents an external, an internal and a basal surface. Externally with the exception of the superior occipital sulcus the occipital lobe is entirely smooth. The superior occipital fissure runs at right angles to the external occipital fissure. Externally the occipital lobe is separated from the parietal by the par-occipital fissure. The inferior occipital fissure separates the occipital from the temporal lobe. The mesial surface of the occipital lobe presents the cuneus, bounded in front by the parieto-occipital fissure and behind by the calcarine.

The Limbic Lobe.

The limbic lobe is bounded above by the calloso-marginal fissure, posteriorly by the rudimentary post-limbic sulcus, and inferiorly by the collateral fissure. This lobe includes the hippocampal and the fornicate gyri. The gyrus fornicatus

extends from the genu of the corpus callosum to the lower border of the splenium. Here it becomes the hippocampal gyrus. The latter is limited above by the collateral sulcus. In Macacus as in man the hippocampal gyrus forms a convolution of the temporal lobe, and is fused with the rest of hemisphere. In the brain of the sheep this is not the case; the hippocampus has no connection whatsoever with the exterior of the brain. In QUAIN'S "Anatomy of the Human Brain" BEEVOR is quoted as saying that the hippocampus major of apes receives no fibres whatsoever from the lyra of the fornix. To determine this point I carefully dissected two brains of Macacus and found in both a distinct band of fibres running from the lyra of the fornix to the hippocampus major,

The island of Reil in Macacus consists of two convolutions derived from the orbital surface of the frontal lobe. As in man the insula is overlapped by the operculum, and is thus invisible on the exterior of the undissected brain. In carnivores owing to the non-development of a large temporo-sphenoidal lobe, no insula exists.

The Lateral Ventricles.

The lateral ventricles of Macacus are especially interesting owing to the enormous extent to which the posterior cornu is developed. This development is not uniformly attained by man. Numerous cases are on record where the posterior cornu has been of small size or rudimentary. In the past year I have seen two brains, one that of a child two years old, the other an adult brain of thirty years, in which the posterior cornu of the left side measured 1.5 cm. and 2 cm. respectively. The right posterior cornu was well-developed in both cases. The posterior horn of Macacus presents a well-developed bulb, but an ill-developed calcar avis. The anterior and the descending cornua present no features markedly different from those of man.

The corpus striatum of Macacus is remarkable in that the lenticular nucleus seems to exceed the caudate in size. As in man the lenticular nucleus consists of three parts, an outer

portion known as the putamen, and two inner divisions called the globus pallidus. In carnivores no such division exists.

The corpus callosum of Macacus is very short. It presents, however, a well-developed forceps major and a forceps minor. The nerves of Lancisi are also plainly discernible. These cannot be differentiated in the dog. The splenium of the corpus callosum sends off a thick bundle of fibres which fuses with the hippocampus of both sides and serves as a commissure between them.

The anterior commissure is more extensive than in carnivores. It runs into the temporal lobe. Its termination can be ascertained only by microscopic methods.

The Third Ventricle.

The cavity of the third ventricle is extremely small and narrow. This is due to the fusion across the median line of the large optic thalami, which are continuous with one another throughout their length except inferiorly. This fusion across the median line represents the middle commissure of man.

From this brief macroscopic study of the fore brain of Macacus we see that the simian brain closely resembles that of man; for Macacus seems to present most of the conditions existing in man, the sole difference in most instances being one of degree.

DESCRIPTION OF PLATES.

PLATE I.

Fig. 1. The external surface of the left hemisphere of Macacus rhesus.

Fig. 2. Mesial surface of left hemisphere of Macacus rhesus.

PLATE II.

Fig. 1. Mesial surface of the left hemisphere of Macacus nemestrinus.

Fig. 2. External surface of cerebrum of Macacus nemestrinus. Part of the occipital lobe has been removed to show the annectent gyri.

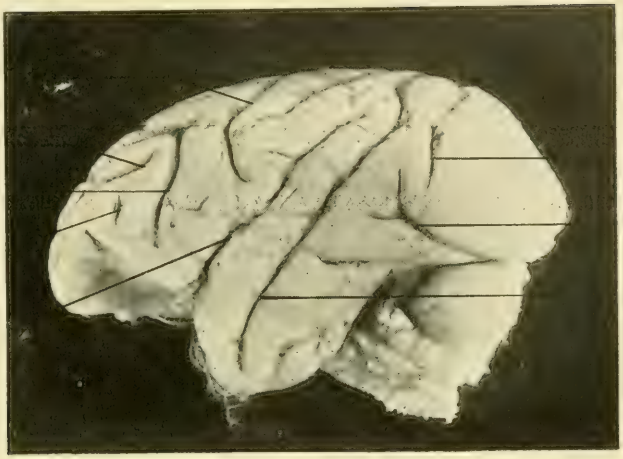

Rolando
Horizontal fissure
Precentral
Rudimentary fissure
Sylvius
Affenspalte
Inferior Occipital
Parallel fissure

Fig 1

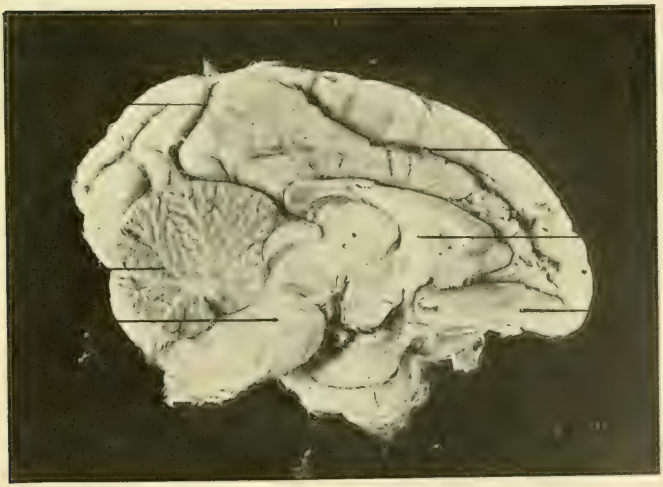

Occipital
Pons
Callosomarginal
Fornix
Frontal Lobe

Fig. 2


Precuneus
Occipital Sulcus
Calcarine fissure
Calloso-marginal

Fig. 1

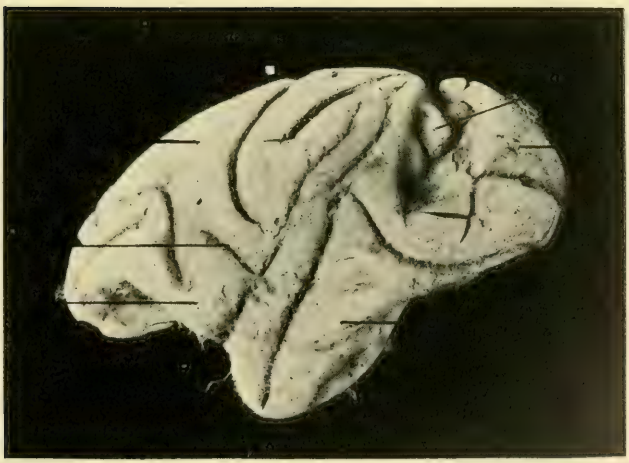

Ascending Frontal
Inf. transverse fissure
Second Frontal
Annectent gyri
Occipital Lobe
Temporal Lobe

Fig. 2

BRAIN-WEIGHTS OF ANIMALS WITH SPECIAL REFERENCE TO THE WEIGHT OF THE BRAIN IN THE MACAQUE MONKEY.

By Edward Anthony Spitzka, M. D.,

Alumni Association Fellow in Anatomy, Columbia University.

(*From the Anatomical Laboratory, Columbia.*)

The accumulation of considerable material for morphological study during a period of over ten years has furnished a series of brain-weights whose publication as a contribution to the subject from a comparative standpoint seems desirable.[1] All the animals whose brain-weights are here given were Mammals (204 in number), the great majority belonging to the Quadrumana, among them being 80 of the genus Macacus. Of the total number, 192 brains were weighed in the fresh state, the remaining 12 after the body had been injected with a zinc chlorid solution. The latter series is tabulated separately. The weights are expressed in grammes. In all cases the brain was severed from the spinal cord at the foramen magnum and weighed with its pial investment. In nearly all cases the body-weight was also recorded, giving the relative as well as the absolute brain-weight. In this connection it must be noted that many of the animals, particularly among the Quadrumana, were quite young, giving ratios of body and brain-weight not generally applicable to the adult animal. Thus, among the gyren-

[1] The writer is indebted to Professor George S. Huntington for the privilege of compiling these data.

cephalic Mammals, we find such ratios as 1:17 for a young Chimpanzee, and 1:20 for a young Coati-mundi. Of course, such cases can not be taken as standards any more than they can in the human species, where the new-born babe, with a ratio of 1:8 has relatively five times as heavy a brain as an adult man. Furthermore it must be remembered that in the accession of such material as is comprised in this collection, most animals arrive in a poorly-nourished, half-starved condition, or they have died as the result of wasting diseases; in either case losing considerable body-weight and materially detracting from the value of any computations of any brain- and body-weight ratios. It is fortunate that the brain attains to nearly its largest size so early in life, and that its weight is so slightly affected by starvation and disease, and it is for this reason that the writer ventures to subject the large series of brain-weights of the Macaque monkeys to a special analysis. However, since the body-weight alone as a criterion or as a means of comparison is inadequate, it is our purpose hereafter to record as well the bodily dimensions, such as the length from vertex to heel, or to the root of the tail, and particularly measurements of the head.

The list of brain-weights, with the sex, body-weight, and ratio (the brain-weight is considered as equivalent to 1), follows:

TABLE I.

FRESH BRAIN WEIGHTS.

No	QUADRUMANA	Sex	Body-W't	Brain-W't	Ratio: Brain W. =1
			Grams.	Grams.	
1	Troglodytes niger, juv.	♂	5490	318	17
2	" " "	♀	5560	302	18
	Semnopithecus entellus,	♂	6647	117	57
1	Cercopithecus callitrichus,	♂	3159	64	49
2	" "	♂	2898	57	51
3	" "	♀	1679	64	26
4	" "	♀	845	59	15
5	" "	♀	2140	54	40
	Cercopithecus ----------	♂	1502	62	24
1	Cercopithecus mona,	♂	3001	67	45
2	" "	♀	---------	61	---- ----
	Cercopithecus griseo-viridis,	♂	3202	72	44
1	Chlorocebus sabaeus, juv.	♀	1036	50	21
2	" " "	—	1480	71	21
	Chlorocebus cynosurus,	♂	3880	68.5	57
1	Cercocebus fuliginosus,	♂	---------	97	---------
2	" "	♂	1353	91	15
3	" "	♀	1398	105	13
1	Macacus rhesus,	♂	5190	93	56
2	" "	♂	2620	92.5	28
3	" "	♂	1535	92	17
4	" "	♂	1250	90	14
5	" "	♂	1173	87	13.5
6	" "	♂	2072	86	24
7	" "	♂	1928	86	20
8	" "	♂	1551	82	19
9	" "	♂	1327	81.5	16
10	" "	♂	3079	81	38
11	" "	♂	1350	80	17
12	" "	♂	1672	78.5	21
13	" "	♂	912	78	9.3
14	" "	♂	1400	77	18
15	" "	♂	744	77	9.5
16	" "	♂	1275	76	17
17	" "	♂	897	75	12
18	" "	♂	1079	75	14
19	" "	♂	1106	74	15
20	" "	♂	1602	74	21.5
21	" "	♂	1353	73	18
22	" "	♂	895	73	12
23	" "	♂	1105	73	15
24	" "	♂	---------	72	---------
25	" "	♂	1248	64	19
26	" "	♀	2025.5	98	21
27	" "	♀	1325	95	14
28	" "	♀	1207	89	13.5
29	" "	♀	1905	92	21
30	" "	♀	1900	86	22
31	" "	♀	1667	83	20
32	" "	♀	1461	82	18

No	QUADRUMANA	Sex	Body-W't	Brain-W't	Ratio: Brain-W't =1
			Grams.	Grams.	
33	Macacus rhesus,	♀	1685	81	21
34	" "	♀	2045	80	25.5
35	" "	♀	2286	79	29
36	" "	♀	1747	78	22
37	" "	♀	1626	77	21
38	" "	♀	1656	77	21
39	" "	♀	974	76	13
40	" "	♀	960	75.5	13
41	" "	♀	1187	73	16
42	" "	♀	1106	72	15
43	" "	♀	1760	72	24
44	" "	♀	1942	72	27
45	" "	♀	1388	72	19
46	" "	♀	1342	71	19
47	" "	♀	877	70	12.5
48	" "	♀	1344	67	20
49	" "	♀	1175	67	18
50	" (Tail amputated.)	♀	1880	61	31
51	" "	—	1735	87	20
52	" "	—	cir 2000	87	23
53	" "	—	1749	83	21
54	" "	—	2180	82	26
55	" "	—	1180	82	14
56	" "	—	2020	73	28
57	" "	—	1621	72	22
1	Macacus cynomolgus,	♂	1567	67	23
2	" "	♂	2070	62	33
3	" "	♂	2060	62	33
4	" "	♂	918	59	16
5	" " juv.	♂	582	50	12
6	" " juv.	♂	420	44	9.5
7	" " juv.	♂	540	44	12
8	" "	♀	1203	100	12
9	" " juv.	♀	919	62	15
10	" "	♀	1803	54	33
11	" "	♀	1497	53	28
12	" "	♀	1142	52	22
13	" "	♀	1126	47	24
14	" "	—	1231	62	20
1	Macacus nemestrinus,	♂	8500	128	66
2	" "	♂	8610	122	71
3	" "	♂	5610	119	47
4	" "	♂	4590	118	39
5	" "	♂	---	113	---
6	" "	♂	6620	105	63
7	" "	♀	2287	103	22
8	" "	♀	3580	100	36
9	" "	♀	3100	95	32
10	" "	♀	---	84	---
1	Macacus sinicus,	♂	1340	75	18
2	" "	♂	848	68	12.5
3	" "	♂	703	58	12
4	" "	♀	---	70	---
5	" "	—	---	67	---
1	Macacus pileatus,	♂	1190	60	20

No	QUADRUMANA	Sex	Body-W't	Brain-Wt	Ratio: Brain-Wt =1
			Grams.	Grams.	
2	Macacus pileatus,	♀	1357	72	19
3	" "	♀	1403	64	22
4	" "	♀	1801	62	27
5	" "	♀	1262	57.5	22
1	Macacus speciosus,	♂	5560	98	57
2	" " juv	♀	942	81	11.5
	Macacus melanotus,	♂	1105	80	14
1	Cynopithecus niger,	♂	6350	109	58
2	" "	♂	5490	107	51
3	" "	♀	---	96	--- ---
1	Cynocephalus babouin,	♂	3340	167	20
2	" "	♂	3175	148	21
3	" "	♂	1545	109	14
4	" "	♀	2235	135	16
5	" "	♀	2414	128	19
1	Cynocephalus hamadryas,	♂	10230	199	51.5
2	" "	♀	3332	153	22
3	" "	♀	1678	136	12.5
4	" "	♀	1692	114	15
5	" "	♀	1572	112	14
6	" "	♀	1490	108	14
7	" "	♀	3581	104	34
8	" " juv.	—	---	110	---
9	" " juv.	—	1100	96	11.5
1	Cynocephalus anubis,	♀	5000	152	33
2	" "	—	---	167	---
	Cynocephalus mormon, juv.	♀	1292	103	12.5
	Cynocephalus sphinx,	♀	2481	135	18
	Cynocephalus leucophæus,	♀	1718	124	14
	Mycetes cavaya,	♂	826	45	19
	Mycetes ursinus,	♀	1025	19	54
	Ateles beelzebub,	♀	1870	97.5	20
	Lagothrix humboldti,	—	4850	112	43
1	Cebus capucinus,	♂	2030	79	26
2	" "	♂	1083	76	14
3	" "	♂	1812	70	26
4	" "	♂	1119	58	19
5	" "	♀	1223	68	18
1	Cebus capillatus,	♂	1370	69	20
2	" "	—	1660	77	21.5
3	" "	—	---	67	---
1	Cebus hypoleucus,	♂	672	59	11.5
2	" "	♂	504	50	10
3	" "	♂	585	54	11
	Cebus subcristatus,	♂	902	71	13
	Cebus annellatus (Vertex to root of tail 42 cm.)	♂	(without int's-tin's) 1490	69	22
	Cebus albifrons,	♂	675	58	12
	Chrysothrix sciureus,	♂	2410	22	109
	Nyctipithecus comm.,	—	---	21	---
	Hapale penicillata,	♀	206	8	26
1	Jacchus vulgaris,	♂	320	8	40
2	" "	♂	204	7	29
3	" "	♀	270	9	30
4	" "	♀	298	8.5	35

No	QUADRUMANA	Sex	Body-W't	Brain-Wt	Ratio: Brain-Wt =1
			Grams.	Grams.	
5	Jacchus vulgaris,	—	204	9	23
6	" "	—	150	7	21
7	" "	—	207	7	27
8	" "	—	105	7	15
	Midas ursulus (rufimanus)	♀	361	24	15
	Lemur bruneus,	♂	1505	26	58
	Nycticebus tardigradus,	♂	612	12	51
	Carnivora.				
1	Ursus americanus,	♂	25990	248	105
2	" "	♂	---------	192	—
1	Nasua rufa, juv.	♂	719	35	20
2	" " juv.	♂	---------	30	—
3	" "	♀	3200	41	78
4	" "	♀	2165	32	66
5	" " juv.	♀	1127	29	39
	Lutra vulgaris,	♂	2215	39	57
	Bassaricus astuta,	♂	842	19	44
1	Vulpes fulvus, juv.	♂	3070	49.5	61
2	" " juv.	♀	3458	53	65
	Felis tigrina,	♀	1989	63	31
	Zalophus californ. (Gillespie)	—	---------	335	---------
	Rodentia.				
	Arctomys monax,	♀	3051	11	277
1	Dasyprocta agouti,	♂	---------	16	---------
2	" "	♀	1803	19	95
3	" "	—	2935	21	133
1	Cynomys ludovicianus,	♂	392	7.5	52
2	" "	♀	504	7	72
	Ungulata.				
	Equus caballus,	♀	---------	519.5	---------
	Dicotyles tajacu,	♀	7930	74	107
	Auchenia glama,	♀	---------	222	---------
	Edentata.				
	Myrmecophaga jubata,	♀	18940	84	225
	Tamandua bivittata,	♀	930	21	44
	Marsupialia.				
	Didelphis virginiana,	—	---------	7	---------
	Petrogale xanthopus,	♂	2441	23	106

The following list contains the fresh weight of the body but not of the brain, this organ having been removed some time after a zinc chlorid solution had been injected into the body:

	Sex	Body-W't	Zn Cl 2 Brain-W't
Macacus rhesus,		1866	97.5
" "		2069	86
" "		1490	85
" "		1640	80
" "		805.5	78
" "		978	69
Cercocebus albigena,		1991	76
Cercocebus fuliginosus,		2561	94
Cercopithecus callitrichus,		--------	65
" "		1629	75
Cebus albifrons,		1640	80
Cebus capucinus,		1409	69

ANALYSIS OF 80 FRESH BRAIN-WEIGHTS OF THE GENUS MACACUS.

Macacus rhesus. Among the 57 specimens there are 25 of males, the same number of females, and 7 of which the sex is not recorded. The body-weight is wanting in the case of one of the males. Twenty of the males weighed over 1000 grammes each, and 22 of the the females. Only one of these, a male weighing 5190 gms., with a brain-weight of 93 gms., can be considered a full-grown adult; the ratio is 1:56 and is doubtless much nearer the true adult ratio than any of the others in the list. The cases are tabulated according to sex, and average brain- and body-weight in the following table:

TABLE II.

Macacus Rhesus.

Sex.	No. of Cases	Range of Body-Weight.	Total Body-Weights.	Total Brain-Weights.	Averages. Body-Weight.	Brain-Weight.
Males	20	(1079-5190 gms)	34926.0	1615.5	1746.3	80.77
"	4	(744- 912 ")	3448.0	303.0	861.0	75.75
Females	22	(1106-2286 ")	35659.5	1725.0	1620.9	78.40
"	3	(877- 974 ")	2811.0	221.5	937.0	73.80
(?)	7	(1180-2180 ")	12485.0	566.0	1783.4	80.90
Male	1	----------	----------	72.0	--------	72.00

Ratios of Body-weights and Brain-weights.
(Brain-weight =1.)

Total of 56 cases,	1 : 20.16.
20 Males (1079-5190 gms.)	1 : 21.62.
22 Females (1106-2286 ")	1 : 20.67.

Macacus cynomolgus. There are 14 specimens of this species, 7 of males, 6 of females, and 1 of unknown sex. None of these, to judge by the body-weight, were full-grown animals. The highest brain-weight, 100 grammes, is that of a female weighing only 1203 gms., a case which must for the present be regarded as exceptional. The average weights range between 50 and 67 gms. for the larger animals of the series.

TABLE III.

Sex.	No. of Cases	Range of Body-Weight.	Total Body-Weights.	Total Brain-Weights.	Averages. Body-Weight.	Brain-Weight.
Males	3	(1567-2070 gms)	5697.0	191.0	1899.0	63.7
"	4	(420- 918 ")	2460.0	197.0	615.0	49.2
Females	5	(1126-1803 ")	6771.0	306.0	1354.2	61.2
"	1	(919)	919.0	62.0	919.0	62.0
(?)	1	(1231)	1231.0	62.0	1231.0	62.0

Ratios of Body-weights and Brain-weights.
(Brain-weight =1.)

Total of 14 cases,	1 : 20.87.
3 Males (1567-2070)	1 : 29.82.
5 Females (1126-1803)	1 : 22.12.

Macacus nemestrinus. In eight of the ten members of this species the body-weight had been noted (5 males; 3 females.) Two of the males, weighing respectively 8500 and 8610 gms. have brains weighing 128 and 122 gms., giving ratios of 1 : 66 and 1 : 71.

TABLE IV.

Sex.	No. of Cases	Range of Body-Weights.	Total Body Weights.	Total Brain Weights.	Averages. Body Weight	Brain Weight.
Males	5	(4590-8610 gms)	33930.0	592.0	6786.0	118.4
Females	3	(2287-3580 ")	8967.0	298.0	2989.0	96.0

Ratios of Body-weights and Brain-weights.
(Brain-weight=1.)

Total of 8 cases,	1 : 48.20.
5 Males (4590-8610)	1 : 57.31.
3 Females (2287-3580)	1 : 31.14.

Other Species of Macacus. Five specimens of *M. sinicus*, the same number of *M. pileatus* are all too young to furnish reliable ratios. The average brain-weight of *M. sinicus* (maximum 75 gms.) is 67.6 gms. Of *M. pileatus* (maximum 72 gms.) is 63.1 gms.

An adult specimen of *M. speciosus* (♂) weighing 5560 gms. has a brain-weight of 98 gms., giving a brain ratio of 1 : 57. The brain of a young specimen (♀) weighs 81 gms. A single specimen of *M. melanotus* has a brain-weight of 80 gms.

Judging from these records and allowing for disturbing factors, the following tabulation of the absolute and relative brain-weights, with their variations, may be here proposed. The sexual differences are not discussed at present, for the number of adult specimens is far too small for accurate analysis. As a rule, however, the females seem to have a smaller brain-weight, both absolutely and relatively, although the reverse would appear to be true were the total of the tabulated cases to be alone considered.

The list of "Probable Averages" in Table V is only tentatively proposed, for the accession of a larger number of adult specimens may materially change certain of the figures.

TABLE V.

PROBABLE AVERAGES OF BRAIN-WEIGHTS IN THE GENUS MACACUS.

	Usual Range of Brain-weight.	Probable Average Brain-weight.	Probable Average Adult Ratio.
Macacus rhesus,	70– 90 gms.	80 gms.	1 : 55
" cynomolgus,	50– 70 "	60 "	1 : 50?
" nemestrinus,	95–120 "	110 "	1 : 70
" sinicus,	65– 75 "	70 "	?
" pileatus,	60– 70 "	65 "	1 : 50?
" speciosus,	80–100 "	90 "	1 : 60

A DESCRIPTION OF CHARTS SHOWING THE AREAS OF THE CROSS SECTIONS OF THE HUMAN SPINAL CORD AT THE LEVEL OF EACH SPINAL NERVE.

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A. CURVES SHOWING THE AREA OF THE CROSS-SECTION OF EACH SEGMENT OF THE MATURE SPINAL CORD.

Introduction.

The data which are presented in this paper were gathered for the purpose of preparing a curve based on the human spinal cord, with which to compare the areas of white and gray substance found in the cross sections of the spinal cords of other mammals. Reference to the literature shows that with the exception of the curve presented by Krause and Aguerre (1), which was published while this study was in progress, the series of curves appearing in the text-books and used to show the areas of the gray and white substance at different levels of the cord, was first introduced by Woroschiloff (2), while that investigator was making a study of the conduction paths in the spinal cord of the rabbit. Woroschiloff's curves were based on measurements published by B. Stilling (3).

The fact that the records which Woroschiloff chose as the basis for his curves were from a child of five years, and therefore from a cord not completely developed, has been recently pointed out by several writers. That Woroschiloff should have used these particular records of Stilling, instead of taking the records for mature cords, published in the same vol-

ume, is explained by the fact that only in the case of the five-year old child are the areas for the separate funiculi given, and his interest was at that time directed to the funiculus lateralis. Since the white substance in the cord of the five-year old child is, *both absolutely and proportionately, less than* in the adult, the use of this series of curves to illustrate the gray and white substance in the mature spinal cord is necessarily misleading, yet these curves are at present employed in the text-books, without any accompanying statement to show that they are based on the measurements from an immature cord.

It is intended in this paper to present a chart which shall more accurately show the true relations between the gray and white matter as they appear in the adult, and thus shall replace the older charts now in use. In order to do this, not only should the measurements of the areas be those from the adult spinal cord, but there is another correction which applies to all the charts thus far published, including that of KRAUSE and AGUERRE (1), and which consists in representing the segments of the cord in their true lengths.

I. Representation of the Length of the Segments.

Heretofore, in these charts, the abscissa has always been divided into 31 *equal parts*—each part representing the length of a segment of the spinal cord. Manifestly this will give an incorrect form to the curve, because the segments of the cord are really of unequal length.

As any ordinate representing the area of a cross section applies strictly to the sum of half the distance from it to the ordinates next above and next below the point at which it is erected, it follows that by multiplying the areas represented by any ordinate by the length of the cord to which it applies, we get an approximation of the volume of the segment. It is evident, also, that the volume of a segment thus determined when the divisions of the abscissa are equal, would be different from that determined when the divisions of the abscissa represent the segments in their true length. To make a correct construction, it was therefore necessary to gather data on the

lengths of the segments of the spinal cord. The measurements of these lengths recorded by STILLING (3, p. 619), are insufficient, having been made between the uppermost and lowest fila of each nerve—thus omitting some of the cord, where, as is conspicuously the case in the thoracic region, the line of roots is not continuous. A number of fresh observations were therefore made. The measurements to determine the lengths of the segments in the adult human cord were made on one specimen (W)—preserved in normal size in 10 per cent. formalin;—on the two careful delineations (X, Y) published by KADYI (4), and on the photolithographic chart (Z) of RÜDINGER (5). In the three plates the cord is depicted in natural size. The cords in the order named, are designated W, X, Y, Z.

In the cord W, the condition of the specimen did not permit the measurement of the first four cervical segments. In cords X and Y, the first cervical segment could not be measured on the dorsal aspect nor on the coccygeal segment at all. In cord Z, measurements on the dorsal aspect alone could be made, and even these could not be extended below the level of the 12th thoracic segment.

To determine the length of a segment, the distance between the uppermost fila of successive nerves was found, beginning with the uppermost filum of the first cervical nerve.[1] This was done both on the dorsal and ventral aspects of the cord. In making the measurements, the distance was marked off with a pair of spring compasses, and then this distance was measured on a metal scale to the nearest tenth of a millimeter. Each measurement has been separately entered in Table I.

[1] This method of measurement credits to any segment the entire "intersegmental space" which lies caudad to it. The method of LÜDERITZ (6) was to credit to any segment one-half the length of the intersegmental spaces lying on either side of it. The difference in the results would be the amount by which, in any instance, the intersegmental space caudad to the part of the segment to which the roots were attached differed in length from the sum of half the intersegmental spaces above and below the same parts. This difference in general would be small.

TABLE I.

Showing in millimeters the lengths of the segments in the adult human spinal cord.

Segment Aspect		Cord W Dorsal	Cord W Ventral	Cord X Dorsal	Cord X Ventral	Cord Y Dorsal	Cord Y Ventral	Cord Z Dorsal	Average
Cervical	1				5.9		8.2	7.6	7.23
	2			7.1	12.3	6.0	13.0	10.4	9.74
	3			12.2	11.0	12.0	13.1	13.8	12.40
	4			13.6	11.1	16.1	12.8	18.1	14.34
	5	10.5	11.7	11.9	11.9	14.0	12.6	13.9	12.35
	6	14.3	14.1	13.7	14.0	13.3	13.3	13.5	13.75
	7	12.2	15.4	12.6	15.2	9.8	11.0	13.7	12.85
	8	12.6	15.7	15.6	13.1	10.6	12.7	12.1	13.20
Thoracic	1	12.2	13.3	14.6	13.7	12.9	9.3	13.4	12.80
	2	12.8	14.5	12.9	15.3	13.5	14.1	16.1	14.20
	3	15.4	19.3	18.8	18.8	15.6	16.4	16.6	17.30
	4	16.7	20.2	21.1	19.3	24.6	20.1	24.3	20.90
	5	19.8	19.9	20.3	20.8	23.6	26.0	22.5	21.85
	6	25.8	25.6	24.1	22.2	19.7	25.5	21.9	23.55
	7	28.7	28.8	17.3	20.7	28.4	21.8	23.8	24.22
	8	29.6	28.3	19.8	26.1	23.8	23.8	23.9	25.05
	9	22.8	23.3	19.6	22.4	24.8	26.3	25.7	23.50
	10	23.7	25.4	19.7	21.3	19.6	21.2	26.2	22.50
	11	28.0	20.1	19.1	20.4	23.5	19.3	19.2	21.38
	12	20.2	21.9	20.3	13.9	21.5	19.8		19.60
Lumbar	1	21.3	23.0	15.5	14.7	16.3	19.2		18.30
	2	15.4	13.7	11.0	9.5	15.6	11.9		12.90
	3	13.2	14.0	11.1	9.7	10.8	12.1		11.80
	4	10.8	11.9	10.7	7.8	10.9	11.8		10.64
	5	9.1	7.2	10.5	6.2	9.9	6.1		8.16
Sacral	1	7.5	8.4	10.3	5.5	8.6	6.1		7.74
	2	6.1	6.6	9.6	4.5	13.4	8.3		8.40
	3	6.6	4.4	8.4	4.8	8.3	9.9		7.07
	4	6.1	6.6	5.4	4.7	8.5	8.6		6.65
	5	6.6	4.1	3.3	3.8	4.9	5.9		4.77
Coccygeal	1	2.5							2.50

The last column in the Table (I), gives the average of all the measurements for each segment, and these average lengths were those used for the divisions of the abscissa in the accompanying chart I.

(*a*) *Total Length of the Spinal Cord.* The lengths of all the segments taken together, should, of course, equal the length of the entire cord. The average length obtained for the segments will therefore depend on the lengths of the cords. But before presenting the lengths of the cords which were here ex-

amined, it will be best to state what is already known concerning the length of the human spinal cord.

The correlation in development between the medulla spinalis and the columna vertebralis indicates that the longer columna vertebralis would contain the longer medulla spinalis.

The observations of RAVENEL (7) on the length of the adult human spinal cord, show in 11 adult males, a range in length of 390-480 mm., with an average of 448 mm. In 11 adult females, the range is from 370-460 mm., with an average of 413 mm. These results plainly exhibit the greater average length of the medulla spinalis in the male. The measurements were made on fresh material from the level of the upper edge of the atlas to the lowest filum of the coccygeal nerve on the conus medullaris.

The cords examined for the length of the segments in the present investigation give the following lengths:

TABLE II.

Cord	Sex	Length in mm.
W	Male	458
X	?	403
Y	?	453
Z	Male	448
Average,		440.5

It is thus seen that this average length lies between the average length for the males and that for the females, though rather nearer the former, as determined by RAVENEL (7). It concerns us here, however, merely to show that the average length obtained is a medium one—differences according to sex being disregarded. The average lengths of the segments determined from the several cords (W, X, Y, Z) are presented in Table I. When these average lengths are summed, they give 441.6 mm., for the length of the cord, against 440.5 mm., as determined by direct measurements. The former number is the one employed in the construction of the chart.

LÜDERITZ (6) is the only investigator who has made a detailed study of the length of the segments of the spinal cord.

On comparing the results just given (Table I), with those

obtained by LÜDERITZ (6), it appears that the averages of the sums of the segments in his two men—33 and 37 years of age —show the total to be 450.5 mm., or about 2% more than the total sum in our case. This is a difference which is well within normal limits, since the measurements of RAVENEL (7) show for the male cord a range in length from 390–480 mm. At the same time, the lengths of the segments as determined by LÜDERITZ, agree substantially with our own, when the differences in the total length of the cord and the great individual variations in the lengths of the segments are both taken into account.

This can be shown by the accompanying Table (III), in which the percentage values of the lengths of the different regions of the cord as determined from our own Table (I), and from the observations of LÜDERITZ on two male cords, are compared with the range in the lengths in these regions, as found by RAVENEL in 11 male cords.

TABLE III.

To show the percentage value of the lengths of the spinal cord within the regions named in the table, as compared with the range in these percentages as determined by RAVENEL.

Region.	From Table (I) 2 males, ♂	Lüderitz 2 males, p. 460	Ravenel 11 males, p. 348
Cervical	21.7%	24.1%	19.8–25.0%
Thoracic	55.8%	54.9%	53.2–65.4%
Lumbar	13.9%	11.3%	9.1–13.6%
Sacral and Coccygeal	8.4%	9.6%	1.8–15.2%

For these reasons we are justified in employing our own data in marking off the abscissa for the curve showing areas, since, in so doing, we shall give an approximately true picture of the relations in the human cord of medium size.

For the abscissa, it was decided therefore to take 441.6 mm. and this base line was divided into lengths equal to the average lengths of the segments as recorded in Table I.

II. Areas of Cross-Sections.

In the first instance charts were drawn life size, so to speak, with the abscissa 441.6 mm. long. The ordinates were drawn

on a scale of one linear millimeter for each square millimeter in the area of the transverse section of the cord. The original charts thus made, were too large to publish, and have therefore been reduced photographically to exactly one-third their linear dimensions. As a consequence of this reduction, multiplying the length of the ordinates in the accompanying chart by three, will give a line as many millimeters long as the section has square millimeters of area, and multiplying the length of any segment in the chart by three will give the length of the segment as represented in the column of averages in Table 1.

The data for the areas of the cross sections represented by the ordinates were taken from STILLING (3) and comprise his measurements on four adult cords.

TABLE IV.

Giving the pages in STILLING's "Neue Untersuchungen über den Bau des Rückenmarks"—1859, where the records are to be found.

Designation of Curve.	Sex.	Age.	Pages.
A	Male	45 years	Page 1098
B	Woman	35 years	Page 1100
C	Woman	25 years	Page 1099
D	Male	25 years	Page 1097

The sections from each segment of these cords are also depicted in Table XXVIII of STILLING's Atlas (1859).

This is the place to call attention to the condition of the cords measured by STILLING. All of the measurements of areas used in this present article—including those on the immature cords to be mentioned later on—were made on material hardened in chromic acid and preserved in 97% alcohol. STILLING makes a statement of his method on pp. 1032 and 1033, but it appears to be erroneous in that it calls for so large an amount of chromic acid, practically an 8% solution. Preliminary observations made on the spinal cord of the white rat, hardened in chromic acid 0.6%, followed by 97% alcohol, indicate a slight increase in the volume of the cord after this treatment. This suggests that these measurements by STILL-

ING may give a somewhat greater area than would appear in the fresh cord.

Although the exact effect of STILLING's treatment has yet to be determined, it is not to be anticipated that more than a small correction will need to be made for it, and as the several cords used were all treated by the same method, they are comparable among themselves.

In accordance with the measurements of STILLING, three curves were constructed for each individual. These curves represent his determinations for the total areas of each section, as well as the areas of the white and the gray substance, taken separately; all *measured at the most caudal level of each segment.*

To obtain a general expression for these several measurements, a composite curve—the first on the chart—was made from the averages of the four individual records.

This composite curve shows the maximal total area of the cord to occur at the VI cervical segment, the next greatest areas being at the III lumbar and V Lumbar, a result dependent on the large area of the white substance in C VI, of both gray and white in L III; and of the gray in L. V.

B. ON THE VOLUME OF GRAY MATTER IN THE SEVERAL SEGMENTS OF THE CORD.

A special feature of this chart as now plotted, is that it enables us to estimate the volume of gray substance belonging to the several segments. This volume was determined as follows:

For the first segment we multiply the number of square millimeters represented by the ordinate, by the number of millimeters representing the length of the segment. In the case of the first segment of the cord, the result is probably a trifle too large. Below the first, we can make a more accurate determination of the volumes by using to represent the area one-half of the sum of the two ordinates limiting each segment; this area being multiplied by the length of the segment intervening. Working in this way, the following results have been obtained for the average volumes of gray substance in the segments of the cord as exhibited in the composite curve on Chart I.

TABLE V.

Giving in cubic millimeters the volume of the gray substance in each segment of the mature human spinal cord. With the exception of the first cervical segment, the volume is obtained by multiplying one-half the sum of two limiting ordinates by the length of the intervening segment, based on the data used for the composite curve in Chart I.

	Segment	Volume in cubic mm.	Volume in cubic mm.
Cervical	I	129	
	II	157	
	III	178	
	IV	220	Cervical segments IV-VIII 1220
	V	224	
	VI	275	
	VII	261	
	VIII	240	
Thoracic	I	177	
	II	147	
	III	141	
	IV	148	
	V	171	
	VI	198	
	VII	180	
	VIII	159	
	IX	156	
	X	169	
	XI	178	
	XII	187	
Lumbar	I	216	Lumbar segments I–V. 1086
	II	184	
	III	228	
	IV	256	
	V	202	
Sacral	I	192	
	II	176	
	III	105	
	IV	67	
	V	34	
Coccygeal	I	12	

An examination of the foregoing Table V shows some relations worthy of remark. In the first place, the greatest volume of gray substance is here found in the segment C VI. In the last five of the cervical segments, the total volume of gray substance is 1220 cubic millimeters, being thus decidedly greater than the volume of substance in the five lumbar segments, which contain but 1086 cubic millimeters.

Between the two intumescentiae of the cord, the segment with the smallest volume of gray substance (T III) contains 141 cubic millimeters, which is more than half that in the largest segment, C VI, which contains 275 cubic millimeters.

This shows first, that there is much less difference in the total amount of gray substance in the successive segments of the spinal cord, than would appear by comparison of the areas of their cross sections alone (see composite curve in Chart 1); second, that as a matter of fact, it is the cervical enlargement which contains the greatest volume of gray substance although the area of the gray reaches its maximum in the lumbo-sacral region. It may not be out of place to again call attention to the fact that the division of the base line into equal intervals for the successive segments of the cord, as in the charts based on WOROSCHILOFF'S curves, gives a set of relations which are misleading; for it necessarily suggests that the volumes of the segments are proportional to the areas of their cross sections.

C. RELATION BETWEEN THE AREA OF THE CROSS SECTION OF EACH SEGMENT OF THE CORD OR THE VOLUME OF GRAY MATTER IN IT, AND THE AREA OF THE CROSS SECTION OF ALL THE NERVE ROOTS BELONGING TO THE SEGMENT.

LÜDERITZ (6), p. 478, has published a chart based on STILLING'S measurements, which shows the relations between the combined areas of the cross sections of each of the four spinal nerve roots, and that of the cross section of the gray substance of the segment to to which they belong. The two curves representing the two series of areas run nearly parallel to one another. The data, however, on which the curves are based, are not exactly comparable, for a reference to STILLING (p. 392), shows that the areas of the cross sections of the nerves were taken from measurements in the case of a woman of 26 years; whereas the areas for the cross sections of the gray matter of the cord were from a five-year old child. We have drawn a second curve in which the areas of the gray matter for the mature cord as represented in Table VI, are used. This curve does not fit quite

so closely that for the areas of the nerves, as does the curve based on the areas of the gray substance in the five-year old cord. Especially in the thoracic and lumbar regions, the area of the gray substance is larger in proportion to the cross sections of the nerves than in the case of the young cord. In general there appears to be in the mature cord, as contrasted with that of the child, a shift of the larger areas of the gray substance one or two segments cephalad. As a consequence, therefore, using data derived entirely from mature individuals, the curves are less similar than the figure of LÜDERITZ (Fig. 2, p. 478) would indicate.

If we now compare the relative development of the volumes of the successive segments of the cord, with the areas of the cross sections of the spinal nerves, we find that while there is a fair correspondence in the cervical and in the sacral regions, that in the thoracic and upper lumbar regions, where the segments have grown most in length, a great disparity exists between the volume of the gray substance and the area of the cross sections of the nerves, the gray substance being much more abundant than we should expect. This suggests that in these localities, the lengthening of the segments, and consequent increase in the volume of the gray substance, is merely one of adaptation to the elongation of the vertebrae, and not accompanied by any corresponding increase in the complexity of its structure.

D. GROWTH CHANGES.

I. On the Areas of the Cross Sections of the Several Segments of the Spinal Cord at Different Ages.

For this comparison we have used as a standard the records which were employed for the composite curve in Chart I. As previously explained, the data for this composite curve were obtained by taking the average of the observations on the four individuals used for the construction of curves A, B, C, D respectively of Chart I. The numerical data are given in the column headed "Mature" in Table VI.

To compare with the composite curve we have from

STILLING a series of measurements of the areas of the gray and white substance at the level of the several segments of three immature spinal cords: from a child at one year, from one at two years, and from one at five years. STILLING's tables containing these records are found on pages 1101, 1102, 339 and 343 of his "Neue Untersuchungen über den Bau des Rückenmarkes." 1859.

In the following Table (VI) which contains STILLING's measurements, it is at once seen that certain segments in the five-year old child were not measured. In order to make this table comparable with the others, an interpolation for the missing records, C I and C II and L I and L II, has been made on the assumption that in the five year old cord the areas of the unmeasured segments would form the same fraction of the sum of all the areas that they do in the one and two year old cord. At the foot of the five year old columns in Table VI, the total given is the one obtained after the above interpolation. Moreover, it will be noted that in this cord identical measurements are given for the thoracic segments T.III-VIII and T.IX-XI.

Individual measurements for these several segments would, of course, have been preferable, but there is no reason to suspect that any serious error has resulted from the method here employed by STILLING.

TABLE VI.

Areas of Cross-Sections of the Human Spinal Cord at Different Ages. The records for the cords at 1, 2 and 5 years are copied from STILLING. The record for the cord at maturity gives the averages of his four tables of measurements on adults.

	Areas of White Substance. sq. mm.				Areas of Gray Substance. sq. mm.			
	Age.				Age.			
Segment.	1 yr.	2 yrs.	5 yrs.	Mature.	1 yr.	2 yrs.	5 yrs.	Mature.
Cervical.								
I	31.46	30.75	58.04	62.03	7.07	7.42	12.37	17.85
II	28.98	30.04		68.57	4.60	4.60		14.49
III	22.62	23.33	32.75	72.37	4.60	4.60	11.25	14.14
IV	48.08	41.36	34.65	74.94	18 03	16.26	12.73	16.52
V	45.60	41.36	42.02	73 97	21.21	16.26	19.67	19.70
VI	46.31	37.12	42.02	79.18	20.86	20.85	19.67	20.32
VII	47.37	43.83	40.39	71.84	18.03	14.14	18.24	20.38
VIII	39.24	46.66	33.99	65.30	16.97	12.37	13.68	15.99
Thoracic.								
I	30.75	30.04	28.59	63.65	6.01	6.36	6.97	11.66
II	26.51	26.51	24.12	53.64	6.72	7.78	5.32	9.01
III	20.85	28.99	24.12	52.23	4.95	6.36	5.32	7.24
IV	21.56	26.16	24.12	52.22	5.30	4.95	5.32	6.89
V	22.98	20.50	24.12	50.10	5.30	6.01	5.32	8.74
VI	21.56	22.98	24.12	45.20	4.60	6.36	5.32	8.04
VII	19.44	24.04	24.12	47.43	5.66	5.30	5.32	6.80
VIII	20.86	20.50	24.12	45.15	6.01	5.30	5.32	5.92
IX	20 15	20.85	23.83	40.74	5.66	7.78	4.56	7.33
X	23.68	16.97	23.83	43.05	4.95	7.07	4.56	7.71
XI	23.68	23.33	23.83	41.40	6.36	7.07	4.56	8.92
XII	22.62	20 85	21.74	44.18	7.42	7.07	6.44	10.14
Lumbar.								
I	22.98	23.33	46.30	44.00	7.42	9.54	20.06	13.51
II	22.62	23.68		49.60	10.96	9.90		15.08
III	22.98	19.09	21.15	48.01	14.85	16.61	13.26	23.59
IV	23.33	22.62	22.34	43.30	15.20	15.91	21.02	24.48
V	20.15	19.80	17.07	43.40	17.68	19.80	24.89	25.01
Sacral.								
I	22.62	20.86	17.18	32.34	15.91	21.56	23.53	24.47
II	20.85	13.79	17.26	19.44	18.38	22.62	23.22	17.41
III	10.61	10.61	9.87	12.25	15.20	13.43	17.21	12.19
IV	10.61	5.66	5.97	8.30	9.19	8.84	10.81	7.86
V	3.89	4.59	2.18	4.77	4.60	3.89	6.01	6.36
Coccygeal.								
I	1.06	1.77	.96	2.38	2.83	2.47	2.70	3.18
Total	766.00	741.97	734.80	1455.07	312.53	318.48	334.65	410.93

In order to compare the records in Table VI, we use the sums of the total areas of the section, obtained by adding the sums of the areas of the gray and white substance, which are tabulated separately.

TABLE VII.

Showing the sums of the total areas in the three immature and one (composite) adult cord, as tabulated in Table VI.

Age.	Sum of 31 Areas.
1 year	1078.53 sq. mm.
2 years	1060.45 sq. mm.
5 years	1069.45 sq. mm.
Maturity	1866.00 sq. mm.

These figures show that from one to five years, there is very little variation in the sum of the total areas. It ranges from 1078.53 sq.mm. to 1060.45 sq.mm. Since this difference appears as a deficit in the two year cord, it is probably the expression of an individual variation. The extreme cases, 1 and 3 years, differ by less than 2%, whereas between five years and maturity, there is an increase in the total area of the sections of nearly 74%. From this it is inferred that the growth changes leading to the larger area at maturity occur at some time subsequent to the fifth year of life.

The analysis can be carried a step further by comparing the relative areas of gray and white substance in the several cases.

TABLE VIII.

To show the percentage values of the sums of all the areas occupied by gray and by white substance at different ages.

	White Substance		Gray Substance	
Age.	Sums of Areas in sq.mm.	Percentage of sums of total areas	Sums of Areas in sq mm.	Percentage of sums of total areas
1 year	766.00	71%	312.53	29%
2 years	741.97	70%	318.48	30%
5 years	734.80	69%	334.65	31%
Maturity	1455.07	78%	410.93	22%

A glance at this table shows that during the first five years, the proportional value of the white substance in the section is about 70%, whereas at maturity it reaches 78%, the gray substance of course showing a correlated variation.

It appears then that from the first to the fifth year, there

is little variation in the relation between the gray and white, and that the change in this relation must occur at some period after the fifth year.

In this connection, it is of interest to determine whether the growth changes leading to the greater total area of the cord segments at maturity are the result of a proportional enlargement in the different regions of the cord. In order to determine this, it is necessary to compute the percentage values of the total areas in the different regions. The results of this computation are shown in the following table:

TABLE IX.

Showing for both the mature and immature cords the percentage value which is represented by the total areas of the segments that constitute the cervical, thoracic, lumbar and sacral and coccygeal regions respectively.

Region.	Age.			
	1 year.	2 years.	5 years.	Maturity.
Cervical	39.05	36.86	36.60	37.92
Thoracic	31.85	33.86	33.18	36.30
Lumbar	16.52	17.02	17.42	17.69
Sacral and Coccygeal	12.58	12.26	12.80	8.09
	100%	100%	100%	100%

From the foregoing Table IX, it appears that after the fifth year, the proportional growth in area has been slightly more rapid in the thoracic region, and less rapid in the sacral and coccygeal, while in the two intumescentiae, the relations at maturity are similar to those found during the first to the fifth year of life. From the end of the first year then, the relative areas of the different regions of the cord change but slightly during subsequent development. The statements which have been made on the basis of the total area can also be repeated for both the gray and the white substance separately, though it is not deemed necessary to publish the computations, as the data for them are found in Table VI.

It must be remembered, however, that from the first to the fifth year of year of life, the medulla spinalis is growing rapidly

in length. From the measurements of RAVENEL (p. 350), we have calculated that the length of the medulla spinalis at one year of age would be about 200 mm., whereas he found in a five-year old boy the length to be 300 mm. Yet, despite this increase in length, the measurements just given show that the transverse diameters remain practically constant. Apparently we have here another example of the tendency of structures to grow first in their long axis before enlarging at right angles to it. It must be remembered, however, that we are without observations on the changes which occur within the limits of the first year.

On looking at Table VI, it is to be noted that the area of the white substance at maturity is nearly 95% greater than it was at five years, while the gray substance is only 23% greater, thus showing the much more rapid enlargement of the white substance. This being the case, it is evident that the curves of WOROSCHILOFF, based on a five-year old child exhibiting in cross section hardly more than half of the white substance in its cord than is present in the adult, necessarily give a false notion of the relations at maturity.

II. Comparison of a Curve, Representing the Areas in the Child's Cord, with the Corresponding Curve for the Cord of the Adult.

It has just been shown that from the first to the fifth year, the areas of the cross sections of the spinal cord remain the same size. It is therefore only necessary to obtain the measurements of the lengths of the segments at some period within these ages in order to construct a curve for the child's cord that may be compared with that for the adult.

LÜDERITZ (p. 471) gives the length of the segments in the cord of a female child of three and a half years. His measurements are presented in the following Table X.

TABLE X.

Lengths of Segments of the Cord as Determined by LÜDERITZ in the Case of a Girl of Three and a Half Years.

	Segment.	Length in mm.		Segment.	Length in mm.
Cervical	I	4.7[1]	Lumbar	I	8.25
	II	5.5		II	6.25
	III	7.0		III	4.5
	IV	7.2		IV	4.1
	V	8.6		V	2.9
	VI	6.8			
	VII	6.3	Sacral	I	3.5
	VIII	6.3		II	3.4
Thoracic	I	5.8		III	3.8
	II	7.25		IV	3.5
	III	7.0		V	3.0
	IV	8.9			
	V	10.3	Cocc.	I	3.0
	VI	11.9			
	VII	13.3			
	VIII	11.75			
	IX	11.5			
	X	9.6			
	XI	9.3			
	XII	7.75			

As will be seen from examining the table, the measurement for the first cervical segment is lacking in the original record, but it has been interpolated here on the assumption that it would have the same proportional value as in the cord at seven weeks. The measurements for a cord at this latter age being given by LÜDERITZ (p. 470), it is possible to make a calculation on this basis, and the result is the number which appears in the Table X. Upon adding the lengths of all the segments together, we find the length of this cord at three and a half years, to be 212.95 mm. For comparison with this result, there is available RAVENEL'S table (p. 550), giving the following individual measurements for the length of the cord in children.

[1] The length for the first segment is interpolated, being given the value of 4.7 mm.

TABLE XI. (From RAVENEL).

Number.		Total Length.
3	Boy of 2 years	245 mm.
4	Boy of 5 years	300 mm.
5	Girl of 9 years	280 mm.

From this comparison it appears that the cord here chosen is short, the child evidently being under size even for a female. However, the length 212.95 mm., is well within the probable limits of normal variability as judged from the variations in the length of the spinal cord in the adult. In using the curve, however, it must be remembered that in this case, the lengths of the segments are from a female cord that is probably short even for this age and sex. This is all that need be said about the base line of curve E. Since the measurements for the areas of the sections of the cord were so similar from the first to the fifth year, it was thought best to choose those made on the two-year old child (Table VI). This record of STILLING was taken because the measurements for all the areas are given, and because it is the middle one of the series of three, and hence we know the form and size of the cord before and after this period.

On examining curve E in chart I, it will be noted that the intervals on the axis of ordinates *are equal to and have the same value*, as in all the other curves in this chart.

Special emphasis is to be placed on this point, and attentention is particularly directed to it, since the designating numbers are smaller in size than those used for the other curves, in which a number is given for each twenty units only. These peculiarities create the illusion that the intervals on the axis of ordinates in curve E are smaller than in the case of the other curves, and for this reason, attention has been called to this point.

On comparing curve E with the composite curve in chart I, some interesting differences appear. If the composite curve be taken as the standard, the following statements may be made. The base line, or length of cord, in E is a little less than half as long. The total area (called *entire section* in chart) at no point rises above 60 sq.mm., whereas in the composite

curve, it runs above 100 sq. mm. The intumescentiae are more abrupt. The enlargements of the areas in the intumescentiae as compared with the areas in the thoracic region, are greater. The maximum total areas in both the cervical and lumbar intumescentiae are further caudad, and the absolute area of the white substance is much less than at maturity. The most marked deficiency in the areas of both gray and white substance occurs in the first three cervical segments, and especially in the third cervical segment. That this last feature is not an individual peculiarity, is indicated by the fact that the one year cord in Table VI (the only cord available for comparison) shows a similar relation. As the curve E is based on a single individual, no significance can be attached to minor peculiarities in it, but enough has been shown by the comparison just made, to indicate that the cord of the child differs from that of the adult in a number of its characters, and that the curves showing the areas in childhood cannot be properly used to show the relations obtaining at maturity.

Conclusions.

The foregoing observations warrant the following conclusions:

The chart given in this article is more correct than that based on the curves of WOROSCHILOFF, since the areas of the gray and white substance are taken from measurements on the mature spinal cord, and are plotted on a base line, the divisions of which are proportional to the lengths of the spinal segments. These curves show the greatest areas at the level of C. VI, L. III, and L. V. The curves, however, are generalized, and apply to a cord of medium size, the differences due to sex being disregarded.

Moreover, the measurements of the areas are from cords which had been hardened in chromic acid, and preserved in alcohol. This treatment has certainly altered the size of the cord, but control experiments indicate that the alteration in size has probably been slight. A study of chart I (see Table V) shows that the volume of gray substance in the intumescentia cervicalis is greater than that in the intumescentia lumbalis.

There is a general correspondence between the area of a cross section of the gray substance at the level of any segment and the area of the cross sections of all the spinal nerves belonging to the segment. When, however, the volume of the gray substance, instead of the area, is used for the comparison, a disproportionately large amount of gray substance is found in the case of the thoracic and upper lumbar segments. This is interpreted as indicating a passive enlargement of the gray substance in these segments of the cords which have been most elongated.

When the cords of immature individuals are compared with those from adults, several important relations are brought to light. In the first place, the sum of the total areas of the cross-sections of the cords, from one to five years, is practically the same (see Table VII), although during the period, a considerable growth in length has occurred. During this time, therefore, growth in the long axis has taken place without any corresponding growth at right angles to the long axis.

The form of the cord from one to five years is nearly like that at maturity, the difference being that in the mature cord the relative enlargement of the areas of the cross-sections has become greater in the thoracic region, but less in the sacral and coccygeal (see Table IX). At maturity, the relative enlargement of the two intumescentiae is practically the same as at the fifth year. From the fifth year to maturity, both the length and the weight of the entire cord as well as the area of the cross-sections at the level of the several segments are increased. The sum of the areas of the white substance at maturity is 98% greater than at five years, and that of the gray substance 23% greater (see Table VIII). This absolute increase must represent either enlargement of elements already completely developed, or the development of elements still immature at the earlier age, or some combination of both of these processes. Yet the failure of the intumescentiae to increase in their relative area in the mature cord (see Table IX), or in their proportional length (RAVENEL, p. 350), would seem to indicate that during this period there

was no increase in their relative complexity; a result, which, to say the least, was unexpected.

On comparing the curves for the areas of the cord at 3½ years (curve E), with the composite curve for the adult, in order to determine the change in the form of the cord due to growth, several important differences appear. In the child's cord, the total areas of the sections are of course less than in the adult; the greater deficiency appearing in the substantia alba. In the child's cord, the intumescentiae are developed more abruptly than at maturity, and the maximal areas appear further caudad; yet, despite this, the sums of the total areas in the cervical and lumbar portions of the cord have almost the same relative values (see Table IX). The most marked deficiency in the child's cord appears in the areas of the first three segments of the cervical region and especially in that of the third cervical segment, while the entire thoracic region is less developed than it will be at maturity. On the other hand, the sacral region is arrested in its later growth and becomes relatively smaller.

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EXPLANATION OF CHART I.

This chart represents by curves, the areas of the cross-sections of several human spinal cords, as well as the areas of the gray and white substance as they appear in each section. The base line in all the charts is just one-third the length of the spinal cord for which it stands, and is divided into lengths proportional to those of the spinal cord segments of which it is composed. For the adult cord, the lengths of the segments given in Table I were used in making the original drawings. On the ordinates one linear millimeter corresponds to one square millimeter of area. In all cases the measurement of the area was made up at the caudal end of the segment. In the order from above downwards, the curves are as follows:

Composite Curve—Based on A, B, C, and D, to give the average of the several areas in the curves named. The curves are generalized and apply to a cord of medium length—441.6 cm. long. The influence of sex is neglected. The average age of the four cases would be 33 years.

Curve A. Man of 45 years. Data for areas from STILLING.

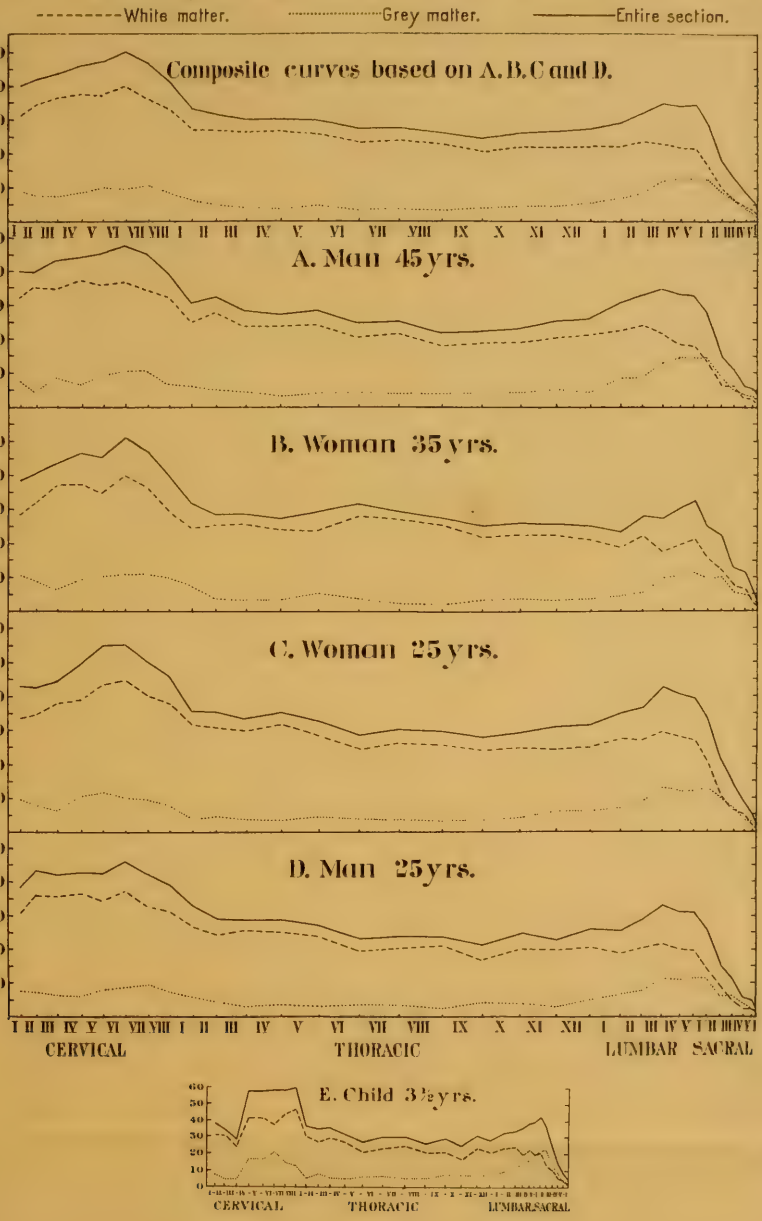
Curve B. Woman of 35 years. Data for areas from STILLING.

Curve C. Woman of 25 years. Data for areas from STILLING.

Curve D. Man of 25 years. Data for areas from STILLING.

Curve E. Child—data for areas from STILLING'S observations on the cord of the two-year old child. Length of segments from LÜDERITZ'S observations on the cord of a three and a half year old girl. Cord rather short.

Curves showing area of cross section of human spinal cord.



To face page 40.]

THE BRAIN OF THE ARCHÆOCETI.[1]

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[A paper read before the Royal Society of London, February 12, 1903.]

So far as I have been able to ascertain, nothing whatever is known of the form of the brain or, more strictly, of the cranial cavity in the Archæoceti. Hence no apology is needed for presenting even this imperfect account of two cranial casts representative of this sub-order, which have come into my hands.

Among the Eocene remains found in the Fayûm region of the Egyptian desert by Mr. H. J. L. Beadnell and Dr. Charles W. Andrews, in 1901, there was a broken skull of *Zeuglodon*,[2] from which it was possible to obtain a mold, representing the form of the greater part of the dorsal and lateral aspects of the brain. A plaster cast was made in the British Museum at the instance of Dr. Andrews, who kindly placed it at my disposal for description.

In the following winter (1902), Mr. Beadnell found in the same locality a natural cranial cast of the same size and general form as the artificial cast of *Zeuglodon*. It is obvious at a glance, if the two specimens be placed side by side, that the natural mold belongs to some member of the Archæoceti,

[1] These notes were originally intended for the Report on the Survey of the Fayûm, to be issued by the Egyptian Survey Department, and are now published separately with the permission of the Under Secretary of State for Public Works and Captain H. G. Lyons, Director-General of the Survey Department.

[2] C. W. Andrews, "Extinct Vertebrates from Egypt," Part II. (Extracted from the 'Geological Magazine,' N. S., Decade IV, vol. 8, 1901, p. 437,—*Zeuglodon Osiris*, Dames'.)

but whether to the same species or even genus as the other specimen must at present remain an open question.

Mr. BEADNELL kindly placed this specimen at my disposal.

The size and relative proportions of the different parts are almost identical in the two casts. Nevertheless, there are a considerable number of differences, some features being displayed in one and not in the other, and *vice versa*. Many of these differences are obviously due to the imperfections of the casts, and especially to the failure of the plaster mold to represent the true form of the brain. But there are several peculiarities of the natural cast—such, for example, as the form of the caudal part of the cerebellum and the shape of the cerebral hemispheres—which are difficult to reconcile with the artificial mold, even if we admit that the inner face of the cranium (from which the latter was made) is damaged or imperfectly cleaned. The differences, nevertheless, are sufficiently pronounced to indicate a generic distinction between the two specimens; and in this connection it is interesting to recall a statement made by Dr. ANDREWS in his first reference to *Zeuglodon*, as "including apparently DAMES' *Z. Osiris*, and perhaps a second species."[1] It would, however, be very unwise, because it would serve no useful purpose, and possibly lead to error, to found a new genus or even a new species on the evidence of this natural cranial cast, when our source of information concerning the known genus (*Zeuglodon*) is as unsatisfactory as that obtainable from the artificial one about to be described. More especially so, when it is remembered that in the case of the only indisputable facts (*i. e.*, size and general form) the two casts are agreed. I shall therefore merely describe and attempt to explain the meaning of the form of the two specimens, and leave the question of the specific identity open for future research.

The general appearance of the brain is extraordinarily peculiar (figs. 1 and 2). The shape of the anterior part of the natural cast (fig. 1, *a* and *b*) closely resembles the cerebrum of

[1] 'Geological Magazine,' September, 1901, p. 401.

a Lizard greatly magnified. An anterior prismatic stalk (*a*), representing the pedunculi olfactorii, suddenly expands into a plump, broad, smooth mass (*b*), showing the form of the chief part of the cerebrum. The maximum breadth of the two hemispheres (fig. 1, *b*) is 95 mm.; the greatest length of each (mea-

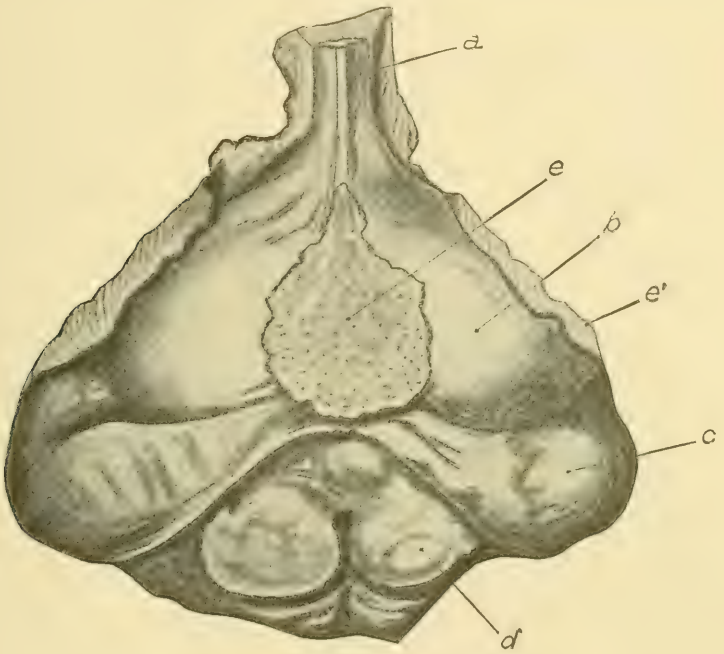


FIG. 1.—Dorsal aspect of the natural cast described in the text. Two-ninths natural size. *a*, olfactory peduncles; *b*, cerebral hemisphere; *c*, *d*, cerebellum; *e*, *é*, fragments of skull.

sured in front from the point where the ventral surface of the olfactory peduncles appear to expand into the chief mass of the hemisphere) is 47 mm.; and the maximum depth is 54 mm. Each cerebral hemisphere (exclusive of the olfactory peduncle) is slightly broader than it is long.

The two olfactory peduncles are represented in the natural cast by a single prismatic process. This extends forward for a distance of 37 mm. (measured along the dorsal edge) in front of the point where the expansion to form the hemispheres com-

mences; and, as the peduncles are broken across there, it is not possible to estimate their total length or the shape and size of the olfactory bulbs.

The coronal section formed by its anterior (broken) surface gives an isosceles triangle with a base measuring 8·5 mm. and sides of 10 mm. each. It expands as it passes backward, so that at its junction with the rest of the hemisphere its sides are each 19 mm. and its base 16 mm. in length.

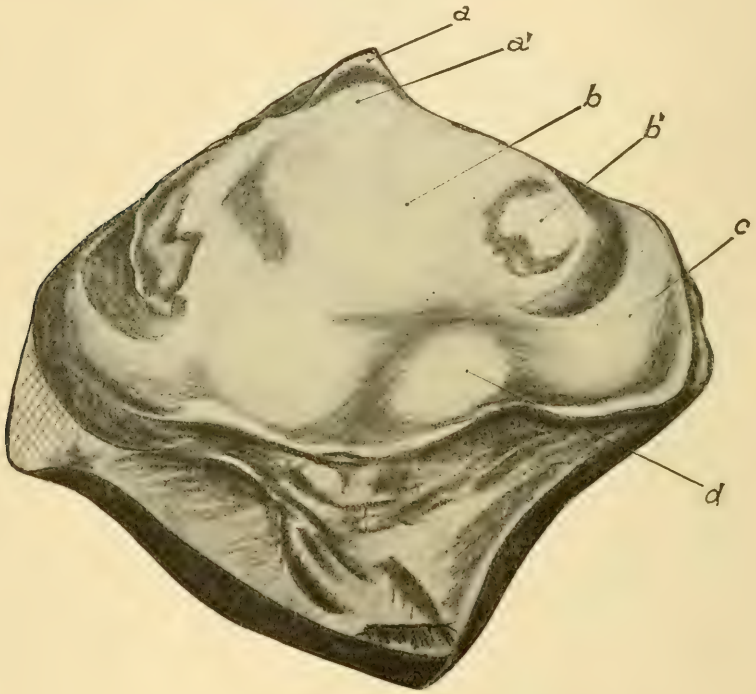


FIG. 2.—Dorsal aspect of the artificial cranial cast of *Zeuglodon*. Two-ninths natural size. *a*, *b*, *c*, *d*, as in fig. 1. *á*, the dorsal rostrum, and *b'*, an irregular boss on the cerebral hemisphere. (These are probably due to imperfections in the cranium.)

In the artificial cast (fig. 2) all that represents this extensive olfactory stalk is an irregular rostrum with two small boss-like projections, one above the other (*a* and *á*). The cerebral hemispheres in the natural cast have a broad base, from which

the sides extend upward toward the narrow dorsal surface with a gradual slope. In the artificial cast, however, the lateral parts of the hemispheres seem to be expanded into full rounded swellings.

Then, again, the antero-posterior diameter of the hemisphere is much shorter (being about 13 mm. less) than it is in the natural cast, although the breadth of the two specimens is approximately the same. It may be that the anterior parts of the skull, from which the artificial cast was made, are so damaged that little reliance can be placed upon the mold as an indication of the exact form of the brain. In fact, if this artificial cast even approximates to the form of the brain, it is quite certain that it did not belong to the same genus as the animal from which the natural cast was derived.

In other words, as we know that the artificial cast belonged to *Zeuglodon*, the probability is that the natural cast furnishes the first evidence of some hitherto undescribed genus of Archæoceti.

Behind the part *b*, which I have just described as the cerebrum, there is (in the natural cast) a large, irregular mass of a very peculiar shape, not exactly comparable to the condition occurring in any other brain known to me.

Immediately behind the hemispheres (*b*) there is a great transverse bar (*c*) measuring 125 mm. in the transverse direction—*i.e.*, extending on each side 15 mm. beyond the lateral margin of the cerebrum (*b*).

Each lateral extremity of this mass (*c*) is expanded to form a large buttress. In the natural cast these buttress-like masses are practically vertical, and of uniform thickness; whereas in the artificial cast they are obliquely-placed, and expanded ventrally. In the natural cast the mesial continuation of these thick lateral masses (each of which measures 30 mm. antero-posteriorly) becomes reduced to a bridge measuring only 5 or 6 mm. [the exact figure cannot be stated, because a piece of bone (fig. 1, *e*) partially covers this region].

In the deep concavity behind the narrow bridge of the area *c* (in the natural cast) two rounded, irregular, walnut-like bosses

project, one on each side of the middle line (fig. 1, *d*). Each of these is 26 mm. in diameter, and is placed so obliquely that its surface looks almost directly backward. Shallow but clearly defined furrows separate these two bodies from each other and from the area *c*. In the artificial cast there is only a very faintly-marked indication of these bodies (fig. 2, *d*).

At a first glance it might seem that they represent the whole cerebellum, in which case *c* would be part of the cerebrum! But careful examination of the natural cast renders such an interpretation highly improbable, and comparison with the artificial cast seems to finally establish the belief that the whole of the region marked *c* forms part of the cerebellum.

It is extraordinarly difficult to accurately interpret this peculiar form of cerebellum. A comparison with other primitive types of cerebellum[1] points to the probability that the lateral buttresses of the mass *c* represent the floccular lobes, and that the walnut-like mass (*d*) represents the cerebellar lobule which I have called "area C" (*op. cit.*, 'Catalogue,' p. 211). If it be objected that the lateral buttress-like mass is much too extensive to be entirely "floccular," attention may be called to the fact that in the large aquatic Sirenia, which have retained an exceedingly primitive type of brain, the floccular lobes are enormous in comparison with those of other mammals (*op. cit.*, 'Catalogue,' p. 346).

It would perhaps be difficult to find elsewhere in the mammalia a greater contrast than that presented by the smooth, reptilian-like cerebral hemispheres of these casts and the highly complicated, ultra-mammalian neopallium of the recent whales, both Odontoceti and Mystacoceti.[2] And yet, if we inquire into the nature of the factors which have molded the form and determined the size of the various parts of the brain in Eocene times and at the present, the contrast between the brain of *Zeuglodon* and the modern Cetacea loses much of its signific-

[1] Compare, for example ('Catalogue of the Royal College of Surgeons,' 2nd edition, vol. 2, 1902), Armadillo (p. 211), Tapir (p. 311), Manatee (p. 346).

[2] *Vide* 'Catalogue of the Royal College of Surgeons,' *op. cit.*, pp. 348—359.

ance, and becomes much less peculiar, even though it may not be wholly explained.

In most Eocene mammals the cerebral hemispheres were exceedingly diminutive in comparison with those of their modern descendants and successors. Moreover, the bulk of the primitive mammalian hemisphere was composed of those parts (hippocampus and lobus pyriformis), which are pre-eminently olfactory; in other words, the neopallium (*i.e.*, that part of the pallium which is neither hippocampus nor pyriform lobe) is especially insignificant. It is a well-known fact that the sense of smell loses much of its importance in mammals of aquatic habits (*e.g.*, *Ornithorhynchus*, the Sirenia, the Pinnipedia, and especially the Cetacea), and in these animals the olfactory parts of the brain dwindle to very small proportions. In the Odontoceti the olfactory bulb and its peduncle actually disappear. The Archæoceti, therefore, are subject to two factors, which will account in some measure for their small cerebrum. For, in addition to the smallness of the brain to which most Eocene mammals are subject, there is their aquatic mode of life. This causes a reduction in size of just those portions of the pallium which form the greater part of the Eocene hemispheres.

In the modern Cetacea the neopallium attains to the greatest absolute size which it ever reaches in any mammal. This fact cannot, however, be considered fatal to the belief in the close affinity of the Archæoceti and the Cetacea, because the extraordinary dissimilarity between the brains in the two sub-orders is such as we know to have been produced by the operation of well-recognised causes in the long lapse of time which separates the dawn of the Tertiary period from the present day. In all mammals which lead a life "in the open" it has become a condition of their survival that the neopallium must increase in size in each successive generation: failing this, the creature must either adopt a "retired and safe mode of life" or become extinct. Numerous examples might be quoted in support of this hypothesis. But the case of the Sirenia shows us how little we really know of the factors which

determine the size of the brain. These creatures began the struggle for existence in Eocene times with relatively large brains, in spite of their aquatic mode of life; and they have been succeeded by generations of descendants whose latest progeny at the present day have a brain-equipment only slightly superior to their earlier Tertiary ancestors (*vide* Catalogue, *op. cit.* p. 344, *et seq.*). Even if we admit that the modern Manatees and Dugongs lead an eminently safe and retired life, which is in marked contrast to the venturesome and "open" life of the whales and porpoises, much still remains to be satisfactorily explained.

Perhaps the most striking feature of the brain of *Zeuglodon* is the extreme disproportion between the size of the enormous cerebellum and the diminutive cerebrum. In this respect the fossil brain presents a most marked contrast to that of all recent mammals, and especially to that of the Cetacea. This relatively great size of the cerebellum is not peculiar to the Archæoceti, but is common to other extinct mammals of large size. In my memoir on the brain in the Edentata[1] the difficulty presented itself of adequately explaining a similar phenomenon in *Glyptodon;* and it must be born in mind, in even attempting to do this, (1) that the obtrusive greatness of the cerebellum presents itself only in large mammals and not in lowlier vertebrates, and (2) that the size of the cerebellum is not proportionate to that of the cerebrum. In the case of *Glyptodon* I four years ago attempted to explain these facts in this manner.

The development of the neopallium in mammals opens up the possibility of the performance of many more complex muscular acts than are possible in the Amphibia or Reptilia; these acts require a co-ordinating mechanism, the size of which will be largely determined by the bulk of the muscular masses, the actions of which are to be harmonised, and the extent of the sensory surfaces which send into the cerebellum streams of controlling impulses. A large cerebellum is being demanded by a

[1] "The Brain in the Edentata," 'Linnean Society's Trans.,' 2nd series, Zoology, vol. 7, part 7, 1899, p. 381.

large mammalian body, even if the cerebrum is small. I cannot offer any more satisfactory explanation of the magnitude of the cerebellum in *Zeuglodon* than this.

It is clear from the foregoing that the extraordinarily great contrast in the appearance of the brain of the Archæoceti and that of the Cetacea cannot be urged as a reason against their kinship, when it is remembered that the operation of known factors is quite sufficient to explain the transformation of the one type into the other in the time which has separated the Eocene period from the present.

Having disposed of these negative arguments, we may consider the positive evidence for Cetacean affinity in the brain of *Zeuglodon*.

The shape of the cerebrum, and especially its relatively great breadth, is peculiar. In fact, this form of hemisphere rarely or never occurs among mammals, other than the Cetacea. I have elsewhere[1] attempted to explain the shortness of the Cetacean hemispheres by the fact that the abortion of the basal (olfactory) parts of the cerebrum limits their longitudinal extension. This, however, is not the whole explanation, because in many microsmatic Sirenia (*Halicore*), and Pinnipedia (*Otaria*, *Phoca*), the hemispheres are not especially broad. The disproportionate breadth seems, in fact, to be to some extent a characteristic of the Cetacea; and, in this respect, *Zeuglodon* agrees with them.

The peculiar elongation of the olfactory peduncles beyond the anterior extremities of the hemispheres is rarely found in mammals, though it is common enough in Reptiles and the Ichthyopsida. In fact, the exact parallel to the condition found in *Zeuglodon* occurs among recent mammals only in the Cetacea.[2] An analogous condition is found in the extinct Lemuroid *Megaladapis* [described by FORSYTH MAJOR (*op. cit.*)] and some *Amblyopoda*.

[1] 'Catalogue of the College of Surgeons,' *op. cit.*, p. 350.

[2] Full references to this are given by FORSYTH MAJOR, "On the Brains of Two Sub-Fossil Malagasy Lemuroids," 'Roy. Soc. Proc.' vol. 62, 1897, p. 48, second footnote.

It is not without interest to note that the two outstanding features of the cerebral hemispheres of the Archæoceti, even if their value as indices of kinship be slight, both find their nearest parallel in Cetacea. There are no characters of the brain of the modern Cetacea which can be regarded as certainly distinctive, if we put aside such features as the extreme dwindling of the olfactory apparatus, and the enormous development of the neopallium. Both must be regarded as late acquisitions, not to be expected in an Eocene mammal. Under these circumstances these slight points of positive evidence of the relationship of the Archæoceti and Cetacea must be allowed some value, as reinforcing the testimony of the skeletal parts.

If we seek to institute closer comparisons between the brain of *Zeuglodon* and of the Odontoceti and Mystacoceti with a view to the determination of its relationships, we are not unnaturally doomed to disappointment. It might, perhaps, be supposed by some anatomists that the absence of an olfactory bulb in the Odontoceti might point to a closer affinity of *Zeuglodon* to the Mystacoceti, in which a small olfactory apparatus is retained. But there is every indication that the olfactory apparatus of the Odontoceti has become aborted quite recently.

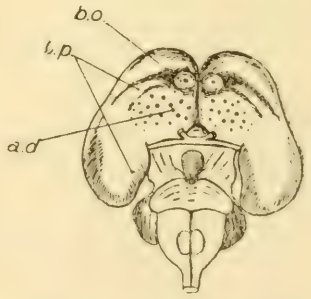


FIG. 3.—Ventral aspect of brain of an early fœtus of *Monodon*. Natural size. *a. d.*, locus perforatus (area desert); *b.o.*, bulbus olfactorius; *l.p.*, lobus pyriformis.

Thus in a specimen of the embryonic brain of the Narwhal (*Monodon*), which was given to me some years ago by Professor HOWES, the remains of the olfactory bulb (fig. 3, *b.o.*) are still

quite visible as a small umbilicate area in part of the "desert region" of BROCA (fig 3, *a.d.*), wherefore it follows that in the early embryo the olfactory bulb and peduncle develop as in all other mammals. Moreover, in all Odontoceti traces of the pyriform lobe are found even in the adult; and in the brain of *Kogia greyi* the rhinal fissure and the typical (macroscopically only) pyriform lobe are retained in a form as clearly defined as that of any macrosmatic mammal (fig. 4). Professor HASWELL, in describing this brain[1] emphasises the fact that "the most re-

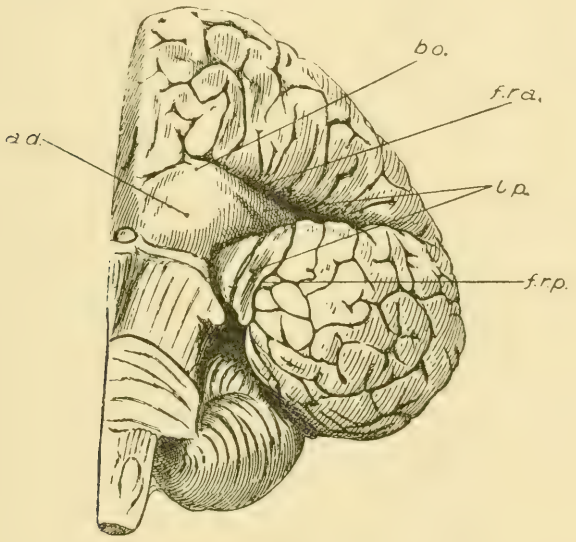


FIG. 4.—Ventral aspect of left hemisphere of *Cogia greyi*. Reduced approximately one-half. *a.d.*, corpus striatum (area desert); *b.o.*, place occupied by bulbus olfactorius in fœtus; *f.r.a.*, fissura rhinalis anterior; *f.r.p.*, fissura rhinalis posterior; *l.p.*, lobus pyriformis.

markable feature of the [basal] region, and perhaps of the whole brain, is in the great depth of the ectorhinal fissure, a feature marking off the present form very strongly from *Delphinus*" (p. 438). Since his illustrations do not properly delineate this interesting conformation, Professor HASWELL

[1] W. A. HASWELL, "On the Brain of Grey's Whale (*Kogia greyi*)," 'Linnean Society of New South Wales Proc.,' vol. 8, 1883 (publ. 1884), pp. 437–439, pl. XXI.

kindly permitted me to examine his specimen; and Mr. J. P. HILL has made me an excellent photograph (of its ventral surface), roughly reproduced the accompanying drawing (fig. 4). It shows the complete and quite-typical rhinal fissure and the characteristic pyriform lobe. In its anterior part the rhinal fissure is fully a centimeter deep.

The exact reproduction of these characters of the rhinencephalon in an adult anosmatic Cetacean, and the presence of the olfactory bulb in the fœtal Narwhal, show that these toothed Cetaceans were certainly (and probably quite recently) derived from ancestors presenting the normal mammalian type of olfactory apparatus. The absence of the olfactory bulb and peduncle in the Odontoceti cannot, therefore, be considered a just reason for adopting the utterly improbable suggestion of a nearer affinity of the Archæoceti to the Mystacoceti than to the Odontoceti.

Estimated by the amount of sand which it displaced, the bulk of the natural cast (including that of a considerable quantity of matrix attached to the base of the brain and some small fragments of bone) is 410 c.c. If the necessary corrections and estimations be made from this gross cubic capacity, the weight of the brain in the Archæoceti must have been considerably less than 400 grammes, and perhaps nearer 300, as against that of the recent Cetacea, which ranges from 455 grammes in *Kogia* (HASWELL) to 4,700 grammes in *Balænoptera* (GULDBERG).

LITERARY NOTICES.

Functional Changes in the Dendrites of Cortical Neurones.[1]

This paper is largely a reprint of a work published in 1897 in the first volume of the Travaux de l'Institut Solvay, whose results the author now regards as fully confirmed and established. Some of these conclusions are as follows:

The pyriform appendages (spines or thorns) of the dendrites of the cortical neurones constitute the terminal apparatus of the dendrites; they increase considerably the surfaces of the nerve cells and play an important rôle in the physiology of the brain, for in the case of severe disturbance the appendages disappear partially or wholly from the affected cells.

Varicosities represent in the adult brain pathological modifications of the nerve cell. They appear abundantly only in course of grave disorders and are rare in the brain of the healthy animal. In the normal adult the dendrites of cortical neurones do not show varicosities, but are thickly set with the pyriform appendages.

In prolonged etherization, or electrical stimulation or fatigue of the cortex the pyriform appendages disappear, while varicosities are present, but these two phenomena are really independent of each other and the appendages may disappear without any trace of varicosities making its appearance. The author concludes from the disappearance of the appendages that these are motile, but is unable to determine the mechanism of their movement. The cortex is never uniformly involved in the reactions to fatigue, etherization, etc., but beside the affected areas are others apparently unaffected. The paper is followed by a list of 14 titles of papers by the same author on related subjects.

C. J. H.

[1] STEFANOWSKA, MICHELINE. Les Appendices des Terminaux Dendrites Cérébraux et leurs différents états physiologiques. *Archives des Sciences Physiques et Naturelles.* Quatriéme période, t. XI, May, 1901.

The Morphological Position of the Chorda Tympani in Reptiles.

It is generally agreed that the Eustachean tube and tympanic cavity of the higher vertebrates are morphological derivatives of the spiracular cleft of the lower fishes. If the chorda tympani of human anatomy runs down cephalad of the tympanic cavity, as commonly taught, then the precursor of this nerve in the fishes, if such there be, should be pre-spiracular. ALLIS [1] has lately called in question the pre-spiracular (pre-tympanic) character of the mammalian chorda and of course the homologous nerve cannot be sought in the fishes until this point is determined. Since the mammalian chorda pursues an exceedingly tortuous course and one difficult of interpretation, it is worth while to notice the conditions in the reptiles.

VERSLUYS in his recent extensive paper [2] describes and figures these relations in several types of Lacertilia and Rhynchocephalia and comes to this general conclusion: "*Die chorda tympani* geht vom Facialis meist an der Stelle ab, wo dieser sich mit dem eben beschriebenen sympathischen Nerven verbindet, das ist caudal von der Columella und an der inneren dorsalen Ecke des Körpers des Quadratums. Sie reicht dann längs der dorsalen und vorden Baukenhöhlenwand auf der medialen Fläche des in die Paukenhöhle vorspringenden Quadratkörpers bis zum Unterkiefer." The detailed descriptions and figures make it very plain that the chorda tympani of reptiles is pre-tympanic and therefore morphologically pre-spiracular; and in the absence of very definite proof to the contrary, we must assume the same condition to prevail among the mammals also. C. J. H.

Mendel and Jacobsohn's Jahresbericht; Fifth Issue.[3]

The issue of this Annual for 1901 reaches us early in 1903 and, like its predecessors, is an indispensable aid to all research workers in all departments of neurology and psychiatry. The plan of the work is the same as in previous issues.

[1] ALLIS, E. P. The Lateral Sensory Canals, the Eye-muscles and the peripheral Distribution of certain of the Cranial Nerves of Mustelus laevis. *Quart. Journ. Micro. Sci.*, XLV. 2, 1901.

[2] VERSLUYS, J. Die mittlere und äussere Ohrsphäre der Lacertilia und Rhynchocephalia. *Zool. Jahr., Abt. f. Anat.*, XII, 1899.

[3] Jahresbericht über die Leistungen und Fortschritte auf dem Gebiete der Neurologie and Psychiatrie. V. Jahrgang. Bericht über das Jahr 1901. *Berlin, S. Karger*, 1902.

Nervous System of Myxine.[1]

Dr. Holm used a variety of staining methods upon strictly fresh material and is therefore in a position to add many details of importance to our knowledge of this critical form. His most serviceable preparations are those stained by the method of GOLGI and by the iron-haematoxyglin of HAIDENHAIN. The histology of the entire brain is considered; but the results, it must be confessed, are disappointing. While the paper contains much of value and is carefully wrought out and clearly arranged, yet the author has apparently failed to make the most of his material. The discussion of the medulla oblongata, comprising about half of the paper, is especially weak, due largely, it would seem, to the neglect of important recent literature, especially that coming from England and America. C. J. H.

Taste and the Fifth Nerve.[2]

The study of five consecutive cases of total removal of the Gasserian ganglion by Krause's operation shows that several weeks after the operation there is a total loss of taste on both the tip and the back of the tongue on the operated side. The author concludes that all the fibers of taste reach the brain by the root of the fifth nerve and that none of these fibers reach the brain by either the seventh or the ninth roots. C. J. H.

The Phylogeny of the Pallium.[3]

This volume, for which we are indebted to the kindness of Professor G. Elliot Smith, contains descriptions of the nervous system of the Invertebrata and of the brain and spinal cord of the Vertebrata of the collections of the Royal College of Surgeons. The Invertebrata, spinal cords of Vertebrata and brains of Fishes, Amphibia and Birds are described by Mr. R. H. Burne; the brains of the Reptilia and Mammalia by Professor G. Elliot Smith, assisted in the Primates by Mr. W. L. H. Duckworth.

[1] HOLM, JOHN F. The Finer Anatomy of the Nervous System of Myxine glutinosa. *Gegenbaur's Morph. Jahrb.*, XXIX, 3, 1901, pp. 365-401.

[2] GOWERS, W. R. Taste and the Fifth Nerve. *Journ. of Physiol.* XXVIII, 4, July, 1902.

[3] Descriptive and Illustrated Catalogue of the Physiological Series of Comparative Anatomy contained in the Museum of the Royal College of Surgeons of England. Second Edition. Vol. II. *London:* Taylor and Francis, 1902, pp. x, 518.

The volume, we should say, is very nearly an ideally perfect catalogue. With its lucid descriptions and exceptionally clear wood cuts it is of great value as a work of reference even to those who do not have access to the specimens which it describes.

At the end of the descriptions of the brains is a summary which we venture to quote in full.

The human brain is by no means the largest known to us. The Elephant and the Great Whales possess much larger organs, and even the extinct Sirenian *Rhytina* was provided with a brain of larger absolute dimensions than that of Man. In the case of these huge animals the enormous mass of the brain is probably to be explained by the fact that the increase in size of the surface of the body necessitates a corresponding growth of the neopallium (to which the great proportions are chiefly due), which is the ultimate receptive-organ for sensory impressions.

In the case of the human brain, however, the Anthropoid Apes (which approach near to Man in bodily dimensions) afford us a criterion as to the amount of neopallium which may be regarded as "necessary" (in the Family Simiidæ) for the reception of impressions coming from such an extent of sensory surface as Man possesses. When it is remembered that the largest Ape's brain is approximately half the size of the smallest normal human brain, and the average Gorilla's brain only about one third (approximately) the weight of the average European's brain, it will then be understood how great an area of neopallium (to which the disproportionate size of the human and Anthropoid brains is chiefly due) Man possesses over and above the needs of the average member of the Simiidæ, to serve as the physical basis (so to speak) of an associative memory of immeasurably greater potentialities (for storing and comparing sensory impressions) than that of any other animal. The feature, therefore, which distinguishes the human from all other brains is the relatively enormous size of the neopallium in comparison with the minimum which the forces of natural selection have made a condition of survival in a member of the Simiidæ. [1]

The neopallium assumes important functions and becomes a condition of survival for the first time in the Mammalia, and in each successive epoch it has become incumbent upon every mammal either, on the one hand, to adopt some eminently safe mode of life or some special protective apparatus to avoid extinction, or, on the other hand, to "cultivate" a larger neopallium, which, as the organ of associative memory, would enable it to acquire the cunning and skill to evade danger and yet adequately attend to its needs. In many of the Eocene Mammalia (*cf.* the cranial cast of *Dinoceras*) the neopallium is reduced

[1] I use the term "neopallium" (Journ. Anat. and Phys. vol. xxxv, 1901, p. 431) because the other parts of the pallium, *i. e.* the hippocampus and pyriform lobe, do not share in this increase. [The significance of the term "neopallium" is explained in the article here cited. Cf. also the abstract in this JOURNAL, vol. XII, p. xii.—C. J. H.]

to such diminutive proportions that the brain resembles the reptilian type; and in each successive generation the neopallium becomes larger or the creature, in self-defence, is compelled to adopt some safe form of life. The *Hippopotamus* and the Sirenia are examples of mammals which have not kept pace in the fierce race for neopallial supremacy but survive by adopting habits of life which are eminently safe. The condition of the human brain represents the other extreme. Here the neopallium has attained its maximum development, and its possessor has not had to seek refuge either in a retired mode of life or by any protective specialisations of structure either for offence or defence, but has attained the dominant position in the animal kingdom, whilst retaining much of the generalised structural features of a primitive mammal.

This expansion of the neopallium is general and not restricted to any localised areas. Thus we cannot say that the greatness of the human neopallium is to be wholly attributed to a growth of the frontal or of the parietal or of the occipital areas, as various writers have maintained; because all parts exhibit distinct evidences of extension. But some regions exhibit the effects of this general expansion more decisively than others, and many writers have assumed (quite erroneously, I believe) that such effects are to be attributed to localised growth. [1] Thus there are very noteworthy evidences of growth in the region around the insula in the human brain, but this is probably for the most part an expression of the general extension in a region which lends itself to a clear demonstration of any increase.

In the early mammals the olfactory areas form by far the greater part of the cerebral hemisphere, which is not surprising when it is recalled that the forebrain is in the primitive brain essentially an appendage, so to speak, of the smell-apparatus. When the cerebral hemisphere comes to occupy such a dominant position in the brain it is perhaps not unnatural to find that the sense of smell is the most influential and the chief source of information to the animal; or perhaps it would be more accurate to say that the olfactory sense, which conveys general information to the animal such as no other sense can bring concerning its prey (whether near or far, hidden or exposed), is much the most serviceable of all the avenues of information to the lowly mammal leading a terrestial life and therefore becomes predominant; and its particular domain—the forebrain—becomes the ruling portion of the nervous system.

This early predominance of the sense of smell persists in most mammals (unless an aquatic mode of life interferes and deposes it: compare the Cetacea, Sirenia, and Pinnipedia for example) even though a large neopallium develops to receive visual, auditory, tactile, and other impressions pouring into the forebrain. In the Anthropoidea alone of non-aquatic mammals the olfactory regions undergo an absolute

[1] There is no doubt that localised hypertrophies do occur, but the fundamental distinction of the human brain is the *general* expansion of the whole neopallium.

(and not only relative, as in the Carnivora and Ungulata) dwindling, which is equally shared by the human brain, in common with those of the other Simiidæ, the Cercopithecidæ, and the Cebidæ. But all the parts of the rhinencephalon, which are so distinct in macrosmatic mammals, can also be recognised in the human brain. The small ellipsoidal olfactory bulb is moored, so to speak, on the cribriform plate of the ethmoid bone by the olfactory nerves so that, as the place of attachment of the olfactory peduncle to the expanding cerebral hemisphere becomes removed (as a result of the forward extension of the hemisphere) progressively farther and farther backward, the peduncle becomes greatly stretched and elongated. And as this stretching involves the grey matter without lessening the number of nerve-fibers in the olfactory tract, the peduncle becomes practically what it is usually called, *i. e.* the olfactory "tract." The tuberculum olfactorium becomes greatly reduced and at the same time flattened, so that it is not easy to draw a line of demarcation between it and the anterior perforated space. The anterior rhinal fissure, which is present in the early human fœtus vanishes (almost, if not altogether) in the adult. Part of the posterior rhinal fissure is always present in the "incisura temporalis," and sometimes (D. 710), especially in some of the non-European races, the whole of the posterior rhinal fissure is retained in that typical form which we find in the Anthropoid Apes. When this occurs we can easily recognise the caudal limits of the pyriform lobe, which otherwise becomes confused with the neopallium.

The hippocampal fissure is of a peculiarly consistent nature, and is found in all mammalian brains from *Ornithorhynchus* to *Homo*. The rhinal fissure is equally *sui generis* and almost as constant as the hippocampal. A few small mammals, such as *Notoryctes*, *Chlamydophorus*, *Chrysochloris*, and some small Chiroptera, have no rhinal fissure.

Of the sulci perhaps the most constant is the calcarine, which is found in the Marsupials (both Poly- and Diprotodont), in the larger Chiroptera, *Galeopithecus* (but not in any true Insectivore, nor, strange to relate, Rodent, so far as I am aware), and in all the Edentates, Carnivores, Ungulates, Cetaceans, and Primates. This wide distribution of the calcarine sulcus is not generally admitted, for most writers regard the calcar avis and the calcarine sulcus as the special prerogative of the Primates or even Anthropoidea, and in the celebrated controversy of 1864 the late Professor Owen strove to prove that it was confined to the human brain. It is, however, the most primitive (it may, however, first appear at the same time as the orbital and suprasylvian sulci) and widely prevalent neopallial sulcus in the Mammalia. It makes its appearance in most mammals (soon after the hippocampal and rhinal fissures have developed) as a short oblique sulcus behind the splenium of the corpus callosum (or in the corresponding situation in Marsupials), and hence it is commonly called "splenial" (Krueg) in non-Primate Orders, in which its true nature has not been properly recognised hitherto. [1]

[1] Meynert and Ziehen have called the splenial sulcus "calcarine" in some Carnivores, without indicating any valid reasons for their views. They have

Its subsequent history varies greatly in different Orders. In the Carnivora, Ungulata, Chiroptera, and many other mammals the sulcus becomes concurrent with another element of vastly less morphological importance, which I have called the "intercalary sulcus." The calcarine-intercalary complex forms the "splenial sulcus" of these brains.

In most mammals, with the exception of the Primates, the tension of the growing cortex in the infracalcarine region is relieved by the downward extension of the calcarine sulcus to the neighbourhood of the rhinal fissure.

In the Anteaters, Sloths, Pangolins, Lemurs, and Apes the calcarine sulcus always remains separate from the intercalary sulcus, and the latter joins with the genual sulcus in the Primates to form the callosomarginal sulcus.

In many Carnivores and Ungulates (and in large mammals generally) one or more deep sulci make their appearance behind the calcarine sulcus, and in most cases one of these, which we may call the "retrocalcarine" sulcus, is deeper and more constant than the others and often joins the calcarine sulcus. This is seen to advantage in the brain of the Lion, Tiger, or Seal among Carnivores, or in the Horse, Camel, or Ox among Ungulates. This retrocalcarine sulcus is obviously of very minor morphological importance in comparison with the true calcarine sulcus, and this is shown by its adaptability to the varying mechanical conditions prevalent in different Orders.[1] In the Primates both the retrocalcarine (Cunningham's "posterior calcarine") and the true calcarine (Cunningham's "anterior calcarine") sulci tend, as a result of the occipital extension of the hemisphere, to become horizontal and in most cases become concurrent. In the more rapidly expanding human brain it often happens that the two sulci do not exactly meet, as they generally do in the Apes. Cunningham is thus led to the belief that the human brain differs from the Simian brain in possessing a retrocalcarine sulcus; but there can be little doubt that the so-called "calcarine" sulcus of the Apes is really a fusion of the retrocalcarine and true calcarine sulci, and therefore does not materially differ from the human calcarine complex. If the caudal extremity of this "calcarine complex" be studied in the Apes it will be found to be exceedingly variable and unstable, so that one cannot regard it as a part of the true calcarine, which is an exceedingly stable sulcus.

By true "calcarine sulcus" I mean that depression which corresponds to or produces the calcar avis. As Flower long ago pointed out (Phil. Trans. 1862, p. 198, footnote), the presence of a posterior

attempted to extend its supposed homologies to the Anthropoid pattern so far as to utterly discredit any value that may attach to their recognition of its calcarine nature.

[1] At the same time the fact that it develops in the midst of the region in which Vicq d'Azyr's stripe occurs in the Primates, and which represents the visual "centre," lends a special interest to this sulcus, which obviously accommodates the expanding visual cortex.

cornu of the lateral ventricle is not necessary for the existence of a calcar avis. Thus we find a free calcar in many hemispheres (those of *Orycteropus*, *Thylacinus*, *Pteropus*, for example) in which there is no posterior cornu. But in most mammals the calcar becomes hidden by a great mass of fibres (compare most Carnivores and Ungulates), and cannot therefore be said to exist as a projection *in the ventricle;* and yet in many large Carnivores (*Phoca* for instance) and Ungulates (*Camelus*) a small posterior cornu of the lateral ventricle makes its appearance, and with it a typical calcar again becomes exposed as in the Primates.

It would be strange indeed if the most constant and stable sulcus of the mesial surface of the hemisphere of most mammals should entirely disappear in the Primates, to be replaced by another sulcus presenting identical relations to the lateral ventricle and a similar developmental history, but without being homologous. There is an overwhelming mass of evidence to show that the vertical part of the sulcus generally called "splenial" is the direct homologue of the calcarine sulcus of the Primates.

In many mammals (such as the Lion) the tension of the growing infracalcarine neopallium is relieved chiefly by the downward extension of the calcarine sulcus toward the posterior rhinal fissure, but also partly by certain irregular and inconstant compensatory sulci behind and parallel to this extension. In the Primates, however, the calcarine sulcus becomes very obliquely placed, not only because the occipital region of the hemisphere becomes caudally extended above the cerebellum, but also because the elongating corpus callosum pushes back, as it were, the pericalcarine neopallium; and as a result of this obliquity the sulcus cannot be prolonged towards the rhinal fissure, as happens in the Carnivora and Ungulata, so that the compensatory sulcus, which is known as the "collateral" sulcus, attains a greatly enhanced importance, and fulfils the rôle of the ventral extension of the calcarine sulcus.

A study of the variable collateral sulcus in the brain of Man and the Apes clearly shows its compensatory-calcarine nature.

Another result of the occipital prolongation of the hemisphere is that the calcarine sulcus becomes widely separated from the intercalary (calloso-marginal) sulcus, to which it is joined in most mammals. The stages in this separation are well shown by comparing, say, the brain of a typical Carnivore with those of the *Daubentonia* and the Lemurs. As the result of this separation a new set of mechanical conditions prevail in the area between the calcarine and the calloso-marginal sulci; and, to further complicate matters, the acuate sulcus formed on the dorso-lateral aspect of the hemisphere by the lateral and post-lateral sulci (*i. e.* the intraparietal and its ramus occipitalis transversus respectively) becomes more and more acutely flexed as the occipital prolongation occurs, so that in the Cebidæ the sharp-pointed apex of the V-shaped sulcus so-formed extends toward this region of the mesial wall, which is, for the reasons just mentioned, already in state of "unstable equilibrium," so to speak. As the result two sulci (which may,

however, be concurrent) are formed:—(*a*) a ventral compensatory-calcarine parallel to the calcarine and the dorsal limb of the postcalcarine sulcus, and (*b*) a vertical sulcus cutting into the dorsal edge of the hemisphere. The latter appears to relieve the tension of the extending surface in a region which is obviously influenced by the proximity of the "apex" of the intraparietal sulcus. In some cases (e. g. *Chrysothrix*, D. 554) this sulcus *b* may be joined to the intraparietal, but in most Apes it is independent of it. The two sulci *a* and *b* usually overlap, and in most cases the intervening gyrus becomes submerged so that the two elements appear to form one furrow, which is the "parieto-occipital sulcus." The lattter, therefore, is a complex of two (and often three) new elements; it makes its appearance for the first time in the Anthropoidea in the region between the phylogenetically old calcarine and intraparietal sulci, which are the common heritage of the Meta- and Eutheria. This account will explain the extreme variability of the parieto-occipital sulci in the human brain.

There is yet another remnant in the Primate brain of the calcarine-intercalary junction (which occurs in so many mammals) in the form of a short sulcus above and behind the splenium, which I have called "compensatory" (instead of Broca's misleading title "postlimbic.")

The Sylvian fissure in its complete form is found only in the human brain, and even in Man it often imperfect. It is really a great cleft upon the ventro-lateral aspect of the hemisphere formed by the meeting of the peripheral opercular lips of three sulci, which are quite distinct in origin and in their phylogenetic history. The most stable of these three sulci, and therefore that which takes the chief share in the development of the Sylvian fissure, is that called "suprasylvian" in most mammals. The second is an unstable sulcus analogous to the pseudosylvian sulcus (that which is commonly called the "Sylvian fissure") of the Carnivora and many other mammals. And the third sulcus is the fronto-orbital.

The suprasylvian sulcus is one of the most primitive and constant in the Mammalian series. It is the earliest neopallial sulcus to make its appearance on the external surface of the hemisphere in the course of the development of the Carnivore, Ungulate, and (according to the old observations of Pouchet) Edentate brain, synchronising in this respect with the calcarine sulcus on the mesial surface. Even if its identification is not altogether sure in the Marsupialia (see the accounts of *Thylacinus*, *Macropus*, and *Phascolomys*), we know that it is a most stable sulcus in the Edentata, Rodentia, Carnivora, and Ungulata. In many Mammals it is joined to the less stable postsylvian ("posterior suprasylvian" of most writers) sulcus, which we call "parallel" in the Anthroipodea. In the Great Anteater, however, it usually becomes separated from the latter and joined to a pseudosylvian sulcus to form a Sylvian fissure, not unlike that found in the Lemuroidea. It is significant that in the only case in six hemispheres of *Myrmecophaga* where this junction does not take place, it should also happen that the suprasylvian sulcus is joined to the postsylvian, as in the Carnivora. In *Daubentonia* the supra-

sylvian sulcus is always separate from the pseudosylvian, and is generally joined to the postsylvian sulcus. In the Family Lemuridæ the suprasylvian sulcus is always (or practically always) separated from the parallel (postsylvian) sulcus, but numerous fragmentary sulci, and a backwardly-directed hook at the upper end of the suprasylvian (Sylvian) sulcus, or a forwardly-directed hook to the postsylvian (parallel) sulcus, serve to remind us of the old link between these two sulci, which has been broken.

The lower end of the suprasylvian sulcus in the Lemurs overlaps the upper part of a pseudosylvian sulcus (of the feline type), the gyrus between the two sulci becomes submerged, and the resulting sulcus we now call the "Sylvian fissure." The lower end of the suprasylvian sulcus can be seen in many Prosimian hemispheres emerging from the front of the "Sylvian complex" a short distance above the rhinal fissure.

In the Apes the submerged area increases in extent and is called the "insula.' It is hidden by two opercula; and a comparison of a large series of Ape-brains seems to clearly demonstrate that the dorsal limiting sulcus of the insula is no other than the suprasylvian sulcus.

In no brain does this sulcus extend so far (in the ventral direction) as the rhinal fissure. In many of the larger Apes it emerges slightly and cuts into the anterior lip of the Sylvian fissure. In *Hylobates*, *Simia*, and the *Anthropopitheci* it extends forwards upon the surface so as almost to reach the fronto-orbital sulcus.

The early history of the latter sulcus is not satisfactorily known. It is present in an exceedingly well-developed condition in all the Simiidæ, and in a less obtrusive form in many of the larger Apes; but, on the other hand, it is absent in many of the Cebidæ and Cercophthecidæ. Such being the case, it is very surprising to sometimes find in the Lemurs a small sulcus, which can be no other than the fronto-orbital. It is impossible to say with any degree of probability whether this sulcus is represented beyond the limits of the Primates. The diagonal sulcus of the Carnivora, Ungulata, Edentata (*Bradypus*, *Myrmecophaga*) occupies a position analogous to that of the fronto-orbital in the Primates.

In the Anthropoid Apes there is a pronounced tendency for the anterior lip of this (fronto-orbital) sulcus to become opercular and to extend backward over the insula, the anterior limit of which is marked out by the sulcus itself.

This process of operculation may be carried very far even in *Hylobates*, *Simia*, and *Anthropopithecus troglodytes*; and in one specimen of *Anthropopithecus gorilla* (D. 656) a very close though spurious imitation of the human condition of this region is attained.

In the human brain this process of operculation generally leads to the complete covering of the insula. The anterior lip of the fronto-orbital (or, as we may now call it, anterior limiting sulcus of Reil) grows backward to meet the temporal operculum, and thus gives rise to the "stem" of the Sylvian fissure. The dorsal lip of the forward extension of the superior limiting sulcus grows down to meet the temporal

operculum (thus forming the anterior part of the posterior limb of the Sylvian fissure) and also the orbital operculum (which is the anterior operculated lip of the fronto-orbital sulcus). The latter meeting gives rise to the anterior limb of the Sylvian fissure. It often happens, however, that the expanding cortex in the neighborhood of the meeting place of the anterior and superior limiting sulci becomes accommodated by the formation of an additional operculum—the frontal. As the result two anterior limbs of the Sylvian fissure (instead of one) are produced.

It follows from this account that a complete Sylvian fissure exists only in the human brain, and that the so-called Sylvian fissure of even the Anthropoid Apes lacks properly-constituted anterior limbs, a small part of the posterior limb, and generally also the "stem" of the complete sulcus.

The full development of the opercula leads to the abortion of the upper part of the fronto-orbital sulcus in the human brain.

The lateral, post-lateral, and ansate sulci of the Carnivora and other Mammalian Orders become in the Primates the intraparietal, transverse occipital, and ramus postcentralis superior respectively. It is a moot point whether the coronal sulcus, which is so constant and precocious in the Carnivora, Ungulata, and Edentata, forms the ramus postcentralis inferior of the intraparietal system. The evidence seems to point to the sulcus rectus and the lower part of the central sulcus as being the real derivatives of this furrow.

In most Apes the region lying behind the transverse occipital sulcus undergoes a peculiar modification leading to the formation of a great operculum from the posterior lip of a new sulcus, called Simian or, as the Germans say, "Affenspalte." This does not usually occur in the human brain, probably because the cortical areas around the transverse occipital sulcus undergo a greater expansion than is the case in the Apes.

I have seen, however, in the brain of an Egyptian fellah a small indubitable Simian sulcus like that of the Gorilla. It was separated by a considerable interval from the mesial plane.

It thus happens that this region of the human brain more closely resembles the condition found in many of the larger Cebidæ (in which the opercular formation has either not begun or is only just commencing) than that of the Anthropoid Apes. Of the latter the brain of the Gorilla approaches the human condition much more nearly than does that either of the Chimpanzee or Orang. It must be remembered, however, that the "occipital" and "insular" regions exhibit an extraordinary amount of variation in each of the Simiidæ; the average condition of these two changing areas is much nearer the human type in the Gorilla than in either of the other great Apes.

Of the other sulci of the human brain (besides those already discussed) the only ones which can be called "old" in the phylogenetic sense are the orbital and possibly the inferior frontal sulci.

The orbital sulcus is probably one of the most primitive furrows in the neopallium, if not the earliest. It is the only sulcus found in the

most generalised mammals, *Erinaceus* and *Perameles*. It is a very constant and precocious sulcus in all the Carnivora, Ungulata, Edentata, Cetacea, and many Rodents and *Galeopithecus*. Most writers call it "presylvian" in all these non-Primate orders, but there can be little doubt as to its homology with the orbital sulcus, although, so far as I am aware, such an interpretation has never hitherto been suggested. But it would be strange if this (the most widespread and constant) sulcus of the neopallium should not be represented in the Primates, and there is no other furrow of sufficient constancy in the pararhinal region to represent the presylvian sulcus of other mammals. If moreover we compare such brains as those of *Dolichotis* (Rodent), *Galeopithecus* (Insectivore), *Bradypus* (Edentate), and *Phascolomys* (Marsuipial) with the Lemur's, it is clear that the "presylvian" sulcus of the former can be represented in the Prosimiæ only by the orbital or the fronto-orbital sulcus. Of these the former is not only by far the more constant of the two sulci, but it is also that which occupies the same position and relationship to the rhinal fissure as the "presylvian." A comparison of *Galago* and *Dolichotis* shows this.

If again we compare the behavior of the orbital sulcus in the larger Ungulates (*e. g.*, the camel, horse, and ox) and Carnivores (*e. g.*, the Seals), we shall find that as the hemisphere increases in magnitude (and more especially if at the same time it becomes more microsmatic) the "presylvian" sulcus becomes relegated to a position alongside the anterior rhinal fissure exactly analogous to that occupied by the orbital sulcus in the Gorilla's brain. In man the simple linear orbital sulcus becomes complicated by numerous side branches so as to form triradiate, H-shaped or other patterns; but if a large number of human brains be examined, the orbital sulcus will be found to consist in a very considerable proportion of these cases of a single deep linear sulcus, the apparent branches of which are mere shallow furrows of little importance. Not unfrequently this sulcus joins a small anterior rhinal fissure—thus completing the resemblance to the junction of the "presylvian" sulcus with the rhinal in the Carnivora and others.

The coronal sulcus of the non-Primate mammals may be represented in the inferior frontal and the inferior precentral sulci of Man. One of the earliest sulci to make its appearance in the developing Carnivore and Ungulate brain is the coronal. In the Carnivores it often joins the lateral sulcus, in many Ungulates it is linked to the suprasylvian, in the Pig-family it is united with the intercalary sulcus. In the Primates the so-called sulcus rectus exhibits a similar precocity, and occupies a position not unlike that of the coronal in the Ungulates and the primitive Viverrine Carnivores. It becomes split up in the Cebidæ and Cercopithecidæ into two parts, the sulcus rectus (*sensu stricto*) and the sulcus arcuatus. The former develops into the inferior frontal and the latter into the inferior precentral sulcus.

The problem of the exact interpretation of the central (Rolando's) sulcus presents many difficulties. There can be no doubt whatever as to the homology of the mammalian lateral with the intraparietal sulcus of the Primates, and the interpretation of the ansate as the

ramus post-centralis superior is almost as sure. We find in the carnivora and the Primates respectively a deep and important sulcus bearing the same relations to the ansate and lateral sulci. In the former we call it "crucial" and in the latter "central"; the solution thus naturally suggested is that the central sulcus of the Primates represents the crucial sulcus of the Carnivora. Such a view has often been propounded before, and has in several instances been disregarded for no valid reason. Thus it has been urged (with a singular disregard for the facts of the case) that the crucial sulcus "belongs to the mesial wall," in spite of the patent evidence afforded by the Arctoid Carnivora that when the crucial sulcus becomes dissociated from the intercalary sulcus it often lies *wholly* on the dorsal surface of hemisphere (see the brain of the Bears, the Glutton, and in fact most of the Arctoidea).

If we study the forms assumed by the crucial sulcus in the large Carnivores (such as the Bears and Seals) and by the central sulcus in the large Apes (Simiidæ), we cannot fail to be struck with a striking parallelism, which could only be produced by the operation of similar factors in the two cases. Moreover, the earliest phases of the development of the central sulcus in the Lemurs are similar to the first rudiments of the crucial sulcus in the Viverridæ.

Physiological evidence (which, however, in such matters is notoriously misleading) does not altogether support such an homology. In the Anthropoidea the central sulcus sharply marks the exact caudal limit of the area of excitable cortex, whereas in the Carnivora (so the physiologists tell us) the crucial sulcus lies in the midst of the excitable area.

If we admit the homology of the central and crucial sulci we shall (by comparison with the behaviour of the latter) find an explanation of many features of the former. According to such an hypothesis a glance at a Bear's brain will at once make intelligible the meaning of the superior genu, the caudal bend in the mesial extremity, and the tendency of the central sulcus in the Anthropoid Apes and Man to extend on to the mesial surface in front of the upturned end of the calloso-marginal sulcus.

In the features of its central sulcus (the relative positions of the genua and the behaviour of the mesial extremity of the sulcus) the *Anthropopitheci* approach much nearer to Man than does the Orang or any other Ape.[1]

The human brain is distinguished from those of the Apes by the abundance of sulci between these stable and constant elements.

The superior frontal and especially the middle frontal sulci are much better developed than in the Apes, and innumerable sulci develop in connection with these. The inferior transverse sulcus (so constant

[1] As the result of further investigations since the above was written, I have come to the conclusion that the crucial sulcus represents the dorsal part of the central sulcus and that the ventral part of the latter is formed either from or at the expense of (mechanically) the caudal extremity of the coronal sulcus.

in the Simiidæ and larger Cercopithecidæ) is longer and deeper; and the diagonal sulcus, rarely or never seen in a well-developed form in the Apes, is now almost constantly present as a deep, extensive sulcus, lying between the anterior ascending limb of the Sylvian and the inferior precentral sulcus.

The parietal area is notably much more variable and much richer in secondary sulci than it is in the Apes.

In the temporo-occipital region the "Affenspalte" of the Apes has disappeared, and the depth and extent of the dorsal end of the parallel, the transverse occipital and lateral occipital sulci are correspondingly increased. The inferior occipital, inferior temporal, occipito-temporal, and collateral sulci are usually all present in a well-developed form. In the Apes the deepening and lengthening of any one of these sulci involved a dwindling of its neighbour—a highly developed occipito-temporal sulcus often led to the abortion of the inferior temporal, the disappearance of the anterior end of the collateral, or the curtailment of the inferior occipital or *vice versa;* but in the human brain there is room for all these unstable and mutually compensatory sulci to exist in a well-developed form side by side.

The expansion of the neopallium has far-reaching effects upon other regions of the nervous system: the fiber systems connected with it become more bulky, the cerebellum becomes larger, its middle peduncle—the pons—becomes so broad that it completely covers the trapezoid bodies and extends down to the inferior olives. In innumerable ways the whole nervous system is profoundty influenced and modified in structure as the result, directly or indirectly, of the attainment of the neopallium to the height of its perfection.

Obsessions and Psychasthenia.[1]

In this new work, which, like its predecessors on hysteria and on fixed ideas, deals with large groups of so-called neuroses, P. JANET brings a number of features under a definite heading, the obsessions, impulsions, manias, folly of doubt, tics, agitations, phobias, mysophobias, anxieties, the feelings of insufficiency, neurasthenia and the modifications of the feelings of reality. The very list of these titles gives us a feeling of the confusion that exists in the use of the terms, and we must be grateful to see a more definite entity, after the pattern of epilepsy and hysteria, bring a new order into these conditions so loosely thrown together with neurasthenia. This specialized group is termed psychasthenia. The analysis of the 325 patients has led JANET to the recognition that all these types depend on a lowering of the "psychological tension." Whereas hysteria shows a complete suppression of certain facts and an exaggeration of others,

[1] Dr. PIERRE JANET, Les Obsessions et la Psychasthénie. Vol. I. *Félix Alean, Paris,* 1903.

the psychasthenia shows in the place of this narrowing down of the field of consciousness a lowering of consciousness in its totality, without any complete and localized gaps of anaethesia, anamnesia, paralysis, and without subconscious and subjective elements, and, therefore, with a feeling of the "incompleteness" or insufficiency which is usually absent in hysteria.

The work is of such fundamental importance that an abstract would be too incomplete to be ventured upon. Suffice it to say, that it is a work with which all those must be completely familiar who wish to get out of the hazy vagueness still existing concerning the so-called neurotic conditions.

The second volume will contain the clinical material on which this first volume is built.

With special gratification we note that beside the cross-sections of these conditions, that is, the analysis of the symptom-complex at various times, there is also some help offered in the direction of longitudinal sections, that is, the analysis of the course of the disease from a general clinical point of view. The relations to mental disorders are given with some detail, especially the occurrence of melancholia, of paranoic states, mental confusion and hebephrenia.

The book is dedicated to Th. Ribot, who may well be proud of the work of his pupil. ADOLF MEYER.

McMurrich's Embryology.[1]

This book is, as the title indicates, strictly a text-book of human embryology. It is written largely from the comparative point of view and is quite full on the neurological side, these chapters comprising about one-fifth of the volume. The work is an eminently successful manual, the references to comparative embryology and comparative anatomy tiding the reader over many difficult subjects, notably in the nervous system. We note a few points of criticism.

In the subject of histogenesis advantage is taken of the foundation laid down by the so-called zones of His to contrast sharply the histogenesis of motor and sensory roots and centers in both spinal cord and brain. But the author has failed to carry out this method of treatment as far as possible and so has missed the recognition of the important fact that both dorsal and ventral zones are divisible into somatic and splanchnic zones, whose clear understanding sheds so much light on the

[1] The Development of the Human Body. A Manual of Human Embryology. By J. Playfair McMurrich, Ph.D. *Philadelphia, P. Blakiston's Son & Co.* 1902.

broad morphological plan of the central nervous system. Compare the paper by JOHNSTON on the Functional Divisions of the Central Nervous System in the issue of this Journal for March, 1902.

This failure accounts for the error on p. 408 in homologizing the fasciculus solitarius of the oblongata with the oval bundle and hence with the column of BURDACH of the spinal cord. The components of the peripheral nerves are in a later section correctly given and made excellent use of, and a recognition of the fact that the primary and secondary centers of these components within the brain (especially those of the sensory roots) are likewise clearly differentiated would have shed much additional light on the problems of the functional divisions or zones of the metencephalon.

The differentiation of the ventral plate into somatic and visceral series of nuclei is clearly presented (after HIS) and the visceral (lateral) series is associated with the branchial muscles and their derivatives. This is the traditional view and the one which the reviewer has adopted in his own studies as his working hypothesis; nevertheless it should be recognized that it is not wholly supported by the published facts, especially in the most recent literature, notably the papers of EDGEWORTH. The whole problem of the embryology of the cranial mesoderm of vertebrates requires a renewed investigation and thorough critical analysis.

In discussing the histogenesis of the ventral spinal roots, these fibers are described according to the now current theories as arising wholly from the neuroblasts of the ventral zones of the spinal cord. In view of the constantly recurring evidence of the end-to-end concatenation of cells in the formation of peripheral nerves, some mention should have been made of the "cellular nerve" of the embryo, even though the hypothesis that it participates in the formation of the definitive nerve fiber were rejected.

On page 433, line 14, is an obvious misprint. The word ventral should be inserted before the word motor.

The excellent discussion of the components of the peripheral nerves I would criticise in only one point; viz. the attempt to rank the olfactory nerve and organ as a member of the acustico-lateralis system. This very doubtful homology seems to be a relic of the errors of BLAUE, who endeavored to show that the "olfactory buds" of some fishes represent organs of the lateral line system which had wandered into the olfactory fossa and there differentiated. The futility of this argument was made clear on embryological grounds by MADRID-MORENO in 1886 and later by myself in 1899 (this Journal, Vol. IX, p.

396). The morphological objections are still more serious. In the first place, the structure of the olfactory epithelium is totally unlike that of the organs of the auditory and lateral line systems, where hair cells extending only part way through the epithelium are always present. The methods of stimulation of the two sets of organs are totally different and it is not easy to see how one could have been derived from the other. And finally, all of the acustico-lateralis nerves terminate in the brain in a single center with very characteristic connections, which are totally unlike those of the far distant olfactory center.

At the close of the discussion of the cranial nerves we find this excellent passage: "From what has been said above it is clear that the usual arrangement of the cranial nerves in twelve pairs does not represent their true relationships with one another. The various pairs are serially homologous neither with one another nor with the typical spinal nerves, nor can they be regarded as representing twelve cranial segments. Indeed, it would seem that comparatively little information with regard to the number of myotomic segments which have fused together to form the head is to be derived from the cranial nerves."

On page 458 we read, "Nothing is yet known concerning the development of the various forms of tactile organs," the author having apparently overlooked the papers by SZYMONOWICZ in the Archiv f. mikr. Anatomie, 1895 and 1896.

The adverse criticisms above are, however, relatively insignificant as compared with the general excellence of the discussion as a whole, which is clear and philosophical in design and treatment.

C. J. H.

Motor Nerve Termini in Insects. [1]

The motor nerve terminations in the striated muscles of insects have been studied by various methods by many histologists, among whom may be mentioned ROUGET, RANVIER, FOETTINGER, V. THANHOFFER, CIACCIO, BIEDERMANN, RAMON Y CAJAL and R. MONTI. These investigators have disagreed in many points, but the author divides them into two main classes. The first class includes those, who, like RANVIER, recognize in the striated muscles of insects, as in those of the higher animals, a DOYÈRE'S elevation consisting of granular protoplasmic substance containing more or less numerous nuclei. The nerve fiber, when it reaches this elevation, loses its sheaths, the neuri-

[1] Sulla terminazione nervosa motrice nei muscoli striati degli insetti. Preliminary note by ALBERTO AGGAZZOTTI.

lemma becoming continuous with the sarcolemma, and breaks up into fibrils which pass into the granular substance but do not pass beyond it to enter into relation with the contractile substance of the fiber. The second class is represented by FOETTINGER, who also recognizes a DOYÈRE's elevation under the sarcolemma, containing numerous nuclei. The terminal branches of the nerve fiber, however, according to FOETTINGER, pass through the granular substance and out in different directions, finally fusing with the isotropic or intermediary disk of the muscle fiber. This, then, represents the theory that there is a direct anatomic continuity between the nerve fiber and the muscle fiber.

The author's investigations were made on Hydrophilus piceus and Melolonta vulgaris. He used the haematoxylin method suggested by Dr. C. NEGRO in 1889. The fresh muscles of the wings and legs of the living insects were immersed for 24 to 48 hours in DELAFIELD's haematoxylin solution, washed thoroughly in water, decolorized in a weak acid mixture of glycerine, water and hydrochloric acid. They were then teased and mounted in a medium consisting of equal parts of glycerine and water.

In the insects studied, the motor nerve undergoes dichotomous division of the axis cylinder, the two branches diverging and entering a mass of granular substance which has in profile the form of a cone slightly elevated above the level of the muscle fiber. In the interior of the granular substance, which is stained more or less intensely violet, he finds three or four nuclei which appear granular and stain deeply, resembling the telolemma nuclei described by KÜHNE in the motor plaques of vertebrates. He was unable however to find the so-called sole-nuclei also described by KÜHNE.

While the author has, by this method, confirmed the findings of other investigators regarding the existence of a DOYÈRE's elevation of granular substance containing nuclei, similar to those found in vertebrates, he has as yet been unable to establish several of the most important points in dispute as to the structure of the motor ending in the striated muscles of insects. He has been unable to determine whether the cone-shaped eminence described by him is under the sarcolemma or not and he is not certain from his preparations that the nerve fibrils form in the granular substance a terminal arborization similar to that found in the motor endings in the striated muscles of vertebrates. These points, with the minuter structure of the DOYÈRE's elevation, he reserves for further investigation.

The main interest of the research seems to have centered in the question whether the fibrils end in the DOYÈRE's elevation or pass be-

yond it in a manner similar to that of the ultra-terminal fibers described by RUFFINI. In the twelve preparations described and figured by the author, eight show one or more fine nerve fibrils separating themselves from the main fiber either just before it enters the granular substance or just after it leaves it. These secondary fibrils pass on for variable distances to end either on the same or on a contiguous muscle fiber. He therefore concludes that the motor nerve in the striated muscle of insects does not as a rule end in the DOYÈRE'S elevation, but in the majority of cases passes beyond this, subdividing into a number of fibrillae, which end in other eminences of granular matter either in the same or in one of the neighboring muscle fibers.

While the author has neither, with RANVIER, established the presence of a terminal arborization in the granular sole-plate of the striated muscles of insects, nor, with FOETTINGER, determined a direct anatomic relation between the nerve fiber and the striae of the muscle fiber, he seems, if I interpret his figures and descriptions correctly, to be inclined to favor the view of the latter that the ultra-terminal fibrils, at least, are often closely related to the striae of the muscle fiber. The structure of the motor ending seems, however, from the figures given, to resemble in many respects that of the terminal motor plaques found in the striated muscles of vertebrates and it seems probable that a further study of these endings by some method which more completely stains the terminal nerve fibrils and more perfectly differentiates the nerve and muscle tissues will show a still greater correspondence.

DR. LYDIA M. DEWITT.

The Comparative Anatomy of the Brains of Lemurs and Other Mammals.[1]

Professor ELLIOT SMITH explains in his introduction that this investigation was undertaken primarily to consider the possibility of homologizing the sulci of the cerebral hemisphere in different orders of mammals; but on account of the mass of the material to be considered he has found it necessary to limit this report in two ways, (1) by confining attention to two sulci, the only two which are absolutely constant in all Primates; viz., the calcarine and Sylvian; and (2) by restricting the detailed account of the sulci to the lemurs with, however, extensive comparisons with other mammalian orders.

This account fills 112 pages and is illustrated by 66 text-figures drawn with the beautifully clear, bold outlines characteristic of the

[1] SMITH, G. ELLIOT. On the Morphology of the Brain in the Mammalia, with Special Reference to that of the Lemurs, Recent and Extinct. *Trans. Linnean Soc. of London*, 2 Ser., VIII, Part 10, 1903.

previous contributions by this author. The more important of the conclusions reached are included, along with others, in the extract from the catalogue of the museum of the Royal College of Surgeons given above, and need not be summarized here, save to add one point: "The features of the Prosimian brain become really intelligible only on the supposition that the Lemurs have advanced a considerable distance in the main stream of the evolution of the Primates and have then retrograded; among other manifestations of this retrogressive process many interesting phases of the disintegration of the cerebral sulci are exhibited, so that it becomes possible to recognize the constituent elements of many compound sulci in the Primates, and so the more readily to compare them with the furrows found in other mammals."

C. J. H.

Development of Lepidosiren.[1]

This contribution treats of the general epidermis, buccal cavity, hypophysis, central nervous system and sense organs, and is illustrated by four excellent plates. Notable among the figures are drawings of the brain from different aspects at successive stages, showing also the roots of the cranial nerves. Typical fourth and sixth nerves were found and figured for the first time.

The brain of the adult Lepidosiren closely resembles that of Protopterus. The thalamencephalon and mesencephalon do not become marked off from one another until relatively late and the cerebral hemispheres arise as two separate lateral bulgings of the wall of the thalamencephalon. The most distinctive feature of the contribution is concerned with the histogenesis of the motor nerves, of which we are promised a more full description later. The motor nerve trunks are already laid down at a period when myotom and neural tube are still in close apposition. As development proceeds and the myotom recedes from the spinal cord the nerve trunk lengthens out, increases in thickness, and becomes ensheathed in mesenchymatous protoplasm. At the earliest stage observed the protoplasm of the nerve trunk is continuous with that of the myotom cells, which are provided with tail-like processes extending into the nerve. C. J. H.

[1] KERR, J. GRAHAM. The Development of Lepidosiren paradoxa. Part III. Development of the Skin and its Derivatives. *Quart. Journ. Micr. Sci.*, N. S., vol. XLVI, 1902.

AN ENUMERATION OF THE MEDULLATED NERVE FIBERS IN THE DORSAL ROOTS OF THE SPINAL NERVES OF MAN.

By Charles Ingbert.

With thirty-two Figures.

(*From the Neurological Laboratory of the University of Chicago.*)

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IX. Summary.

I. Introduction.

This investigation was undertaken in order to ascertain the number of medullated nerve-fibers in the dorsal roots of the spinal nerves of man. It was thought that such an enumeration would assist us in determining whether we may postulate separate nerve fibers for each of the forms of dermal sensation, since it would permit us to calculate the average area of the skin innervated by a single nerve-fiber.

II. Historical Statement.

Attempts have been made to determine the value of the roots of the spinal and cerebral nerves as pathways for nerve impulses both by measuring the areas of their cross-sections and by estimating or counting the number of nerve fibers in them.

Limiting our attention to these nerves in man we find that the area of the cross-sections of N. opticus alone has been determined by SALZER (1880)[1], W. KRAUSE (1880)[2], and for the Nn. opticus, oculomotorius, and trochlearis by DONALDSON and BOLTON (1891)[3].

The determination of the number of nerve fibers was made by H. ROSENTHAL (1845)[4] for all the cerebral nerves except N. olfactorius, opticus, and acusticus, by estimations based on the number of fibers counted in a few squares of the ocular-micrometer. TERGAST (1872)[5] made a determination of the number of nerve fibers in the N. abducens, but makes no mention of his method. KUHNT (1879)[6] counted the number of nerve-fibers in a row representing the diameter of the N. opticus, and estimated the entire number by the formula $r^2 \times 3.1416$. KRAUSE (1876 and 1880)[7-8] made determinations for the N. opticus, and (1880)[9] for N. oculomotorius, but does not give his method of estimation.

The area of the cross-section of the roots of the spinal nerves has been determined by KÖLLIKER (1850)[10] and by STILLING (1859)[11].

The only determination on record of the number of fibers

in the roots of the spinal nerves of man is that made by STILLING (1859)[11].

For the purpose of comparison we shall consider the determinations of the areas of the spinal nerves in detail.

III. Determination of the Areas of the Cross-Sections of the Dorsal Roots of the Spinal Nerves of Man.

1. *Kölliker's Determination.* The areas of the cross-sections of the roots of the spinal nerves, as given by KÖLLIKER (1850)[10] for a man and a woman, were in all probability obtained from fresh tissue, as no statement to the contrary can be found. The roots were sectioned between the spinal cord and the spinal ganglia at the place where they penetrate the *dura mater*, (i. e., near the ganglia). After removing the blood vessels and the arachnoidea, he measured the diameters of the roots, including the perineurium, and from these measurements calculated the areas of the cross-sections. That KÖLLIKER was correct in considering his results too large will be seen on comparing them with those obtained by STILLING and myself (Table I [a]). Although the included connective tissue is the chief source of error in his results, yet the fact that he calculated the areas from the diameters of the cross-sections of the nerve roots as if they were perfect cylinders is, no doubt another source of error worth noting. Considering a Paris line (the unit which he employed) equal to 2.2558 mm., I have expressed his results in square mm. in Table I [a].

Although he determined the areas of the cross-sections of the ventral as well as the dorsal roots, the latter only are necessary for our comparison.

2. *Stilling's Determination.* The material used by STILLING (1859)[11] in his determination of the areas of the spinal roots was from the spinal cord of a woman, twenty-six years of age. The roots had been hardened in chromic acid according to STILLING'S method, and sectioned by hand with a razor at the place where they penetrate the *dura mater.* The sections, without staining, were mounted in alcohol. By means of a compound microscope and a camera lucida projections of the

sections were made on paper and the areas determined by two methods:

(a) The projections were lithographed and printed on paper of a uniform thickness, the weight of a square mm. of which had been determined beforehand by several weighings. The outlines of the fascicles in the projections were then cut out and weighed. To obtain in sq. mm. the area of the projection of the cross-section of a given root, the weight of the paper so cut out was divided by the weight of one sq. mm. To reduce the area of projections to the true area of the cross-sections of the roots they were divided by the square of the linear magnification of the projections.

(b) The outlines of the fascicles as projected on paper were measured by means of a planimeter and their areas found in sq. mm. from its readings. The areas of the projections were then reduced to true areas. As the results obtained by the two methods are practically the same, only those determined by the planimeter are given in Table I [a]. His results for the ventral roots are also omitted as not necessary for our comparison.

3. *Author's Determination.* The material used in this investigation was from a middle-aged man, weighing 180 lbs., and killed by accident. The spinal cord, together with the roots, was removed within eight hours after death, and hardened in MÜLLER'S fluid for one month, the fluid being changed every day during the first part of the period of hardening. The dorsal roots of the left spinal nerves were embedded in celloidin and sectioned at the place, between the cord and the spinal ganglia, where they penetrate the *dura mater.*

Although we speak of these roots as all from the left side of this subject, in one instance this was not the case. The dorsal root of Th. IX was from the right side, the one on the left having been injured in removal. The left dorsal root of C. I was wanting in this subject, and the one used was from a different man weighing about 140 lbs. This was obtained for me by the courtesy of Dr. PETER BASSOE. There is, however,

no reason to think that the results of this study are appreciably modified by these facts.

The 20μ thick sections were stained by WEIGERT'S haematoxylin method for the medullary sheath and mounted in dammar. The material was obtained by the courtesy of the Department of Pathology, and the sections were prepared by Dr. IRVING HARDESTY in the year 1901.

To determine the areas of the cross-sections of the roots, projections of the fascicles were made on paper by means of a camera lucida. The areas of these projections were measured by means of a CONRADI planimeter. To obtain the true areas of the cross-sections of the roots from the areas of their projections the magnifying power of the microscope together with the camera lucida used in making them was determined by projecting a micrometer scale ruled in millimeters upon a sheet of paper. In doing this the micrometer slide bearing the scale was placed on the stage of the microscope and so projected that one end of the scale was in the exact center of the projected field (as determined by a perpendicular) and the other end at the periphery of the field. The projected millimeters were marked on the paper and their length gave the magnification sought. The first and second millimeters from the centre were each magnified 68 diameters, while the third, or the one near the periphery, was magnified 69 diameters.

Primary concentric circles were made on tissue paper through the points representing the outer ends of the projected first, second, and third millimeters, and six equidistant secondary concentric circles between the outer two of the primary circles. The tissue paper on which were drawn these circles was superimposed on the projections of the roots so that the centre of these circles corresponded to the exact centre of the projected field of vision (previously determined for the projection of the cross-section of each root) and the fascicles found to lie within the first and second primary circles were considered to be magnified 68 diameters. Those fascicles the centres of which fell within the 1st, 2nd, 3rd, 4th, 5th, 6th, or 7th space (counting towards the periphery) formed by the secondary

circles between the second and third primary circles were considered magnified 68.15, 68.30, 68.45, 68.60, 68.75, 68.90, 69.05 diameters respectively. The actual areas of the fascicles were then found by dividing the areas of the projections of the fascicles by the square of the magnification as determined

TABLE I[a].

Areas in sq. mm. of Cross-Sections of the Dorsal Nerve Roots of the Spinal Nerves of Man.

No. of Spinal Segments		Average length of Segments in mm. according to DONALDSON and DAVIS [14]	KÖLLIKER Male	INGBERT Male	STILLING Female
Cervical	I	7.2	.43	.13	.33
	II	9.7	3.75	2.33	2.18
	III	12.4	2.81	2.14	1.52
	IV	14.3	1.95	2.01	1.39
	V	12.4	3.87	2.82	2.27
	VI	13.8	6.04	4.65	4.41
	VII	12.9	7.06	4.72	3.76
	VIII	13.2	5.75	5.11	4.11
Thoracic	I	12.8	2.81	1.79	2.51
	II	14.2	1.54	.97	1.13
	III	17.3	1.00	.98	0.96
	IV	20.9	1.00	.90	.73
	V	21.9	1.08	.68	.78
	VI	23 6	1.73	.59	.75
	VII	24.2	1.73	.98	.73
	VIII	25.1	1.73	.71	.85
	IX	23.5	1.63	.67	.87
	X	22.5	1.79	.86	.82
	XI	21.4	1.84	.91	.99
	XII	19.6	1.73	1.25	.88
Lumbar	I	18.3	1.90	1.75	1.22
	II	12.9	2.37	2.22	1.50
	III	11.8	2.81	2.53	2.57
	IV	10.6	3.99	2.93	3.49
	V	8.2	4.49	3.20	3.39
Sacral	I	7.7	7.06	3.44	3.96
	II	8.4	3.99	1.92	5.52
	III	7.1	1.11	1.18	2.51
	IV	6.7	.48	.40	1.24
	V	4.8	.23	.13	0.47
Coc.	I	2.5	.04	.03	.11
	31	441.9mm.	79.74	54 93	57.95

above. The measurements of each fascicle were made inside of the connective tissue sheath. The total area for the cross-section of each root is found by adding together the areas of its component fascicles, and is recorded in Table I[a], while the area of each fascicle of the different roots is found in Tables II–XXXII.

4. Comparison of Areas. On comparing the areas of the cross-sections of the dorsal roots as determined by KÖLLIKER, STILLING, and the author, and recorded in Table I[a] we find them as follows:

KÖLLIKER (male)	79.74 mm.
STILLING (female)	57.95 mm.
Author's case (male)	54.93 mm.

KÖLLIKER's areas, it is seen, are considerably larger than those obtained by STILLING and those by the author. This, no doubt, is due chiefly to the amount of connective tissue included by him in determining the areas from the diameters. In looking over my projections in Figs. 2–32 it will be evident at a glance that the amount of connective tissue between the fascicles is a factor of great importance in such a determination.

To test the correctness of this conclusion I have determined by KÖLLIKER's method the area of the cross-sections of the dorsal roots used in my investigation. In doing this I took as their diameters the mean of the two diameters of the projections. The square of the half of this diameter, i. e., the square of the radius multiplied by 3.1416, gives the areas of the projections and this, in turn, divided by the square of the magnification of the projections, or by 68^2, gives 79.14 mm^2 as the true area of the cross-sections of all the left dorsal roots. This harmonizes well with KÖLLIKER's result, which was 79.74 mm^2 for the male. The source of the difference in our results as given in Table I[a] is therefore evident.

On comparing STILLING's areas with those obtained by the author we again find a difference, but not so marked as that between KÖLLIKER's areas and my own. Although STILLING's areas are for a female and mine for a male, his are the larger. We again find the amount of connective tissue included to be a

probable source of error. On examining the projections of the cross-sections of the dorsal roots in STILLING'S Atlas (1859)[12], Table XVIII, we find that he has divided the roots of the 31 left spinal nerves into only 228 fascicles, while, as will be seen from my plates, I divided the same number of roots into 504 fascicles. It is therefore evident that he has included in his results the areas of some connective tissue septa which I have been able to exclude. Another source of difference is the fact that I made corrections for fascicles cut obliquely. In doing this, the number of fibers in a fascicle cut obliquely was divided by the number of fibers per sq. mm. in the nearest adjoining properly cut fascicle providing this had the same appearance as regards the size and density of its fibers. By this means the area of the fascicle in question was reduced to the size of its cross-section when cut at right angles to the fibers composing it. In computing the total area of the nerve this corrected number was the one employed. Where corrections were made the number indicating the uncorrected area is placed in parenthesis in Tables II–XXXII. In the accompanying projections, Figs. 2-32, however, all the fascicles appear drawn with the area which they present in the section. But where it it has been necessary to make a correction in the Tables for the obliquity of the fibers the letter C appears within the fascicle.

The total amount thus deducted from the apparent area of all the roots was 1.389 mm.^{2} Adding this to 54.93 we get 56.39 mm.^{2} as the uncorrected area. If to this we could add the area represented by the connective tissue septa which I have excluded but which STILLING included, my results would probably be a trifle larger than his.

Another source of difference in the results obtained by KÖLLIKER, STILLING, and the author is the amount of shrinkage caused by the reagents employed. The roots used by KÖLLIKER were, as before remarked, most probably not treated with any reagents and should in this respect be normal. STILLING attributes a slight shrinkage to the tissue which he measured, but if this be greater or less than than the shrinkage from the reagents I used there is at present no means for deciding

although it seems probable from the investigations of DONALDSON (1894)[13] on changes caused in the nervous tissues by reagents, that the departure from the normal is but slight.

In order better to compare the areas of the cross-sections already discussed, I have constructed curves. In Fig. 1, Chart I, (page 72) I have constructed curves to compare the absolute areas of the cross-sections of the dorsal roots determined by KÖLLIKER for a male, by STILLING for a female, and by the author for a male. In constructing these curves the normal average length of the spinal cord, 441.6[1] mm., was used as the base line. On this line was marked the normal average length of each segment, as determined by DONALDSON and DAVIS (1903).[14] The ordinates were erected at the caudal end of each segment and each sq. mm. of the area of the cross-section of each dorsal root was represented by 20 mm. on the axis of the ordinates. For publication this chart has been reduced so as to make its base line 96 mm. which is a reduction to 0.22 of the original linear dimensions. In Table I[a] are found the data for this chart.

In Chart II, (page 72) I have compared the same data as are used in Chart I. The base line is the same as before. The ordinates, however, were in this case obtained by taking the largest area in each instance as 100% and expressing the other areas as percentages of this standard. Each percent. in the values thus obtained is represented by 1 mm. on the axis of the ordinates. For publication this chart has been reduced as in Chart I. In Table I[b] are found the data for this chart.

[1] The discrepancy between 441.6 here used and 441.9 in table 1[a] is due to the fact that the latter is the sum of the numbers after being rounded from two decimal places to one.

TABLE Ib.

Showing Percentage Values of the Areas of the Cross-Sections of the Dorsal Nerve Roots as Given in Table Ia. The Greatest Area in each Series is taken as 100%, and the other Areas calculated from this as a Standard.

	No. of Spinal Segments	Percentage Value of Areas. KÖLLIKER Male	INGBERT Male	STILLING Female
Cervical	I	6.0	2.5	5.9
	II	53.1	45.6	37.2
	III	39.8	41.8	27.5
	IV	27.6	39.8	25 2
	V	54.8	55.1	41.1
	VI	85.5	90.9	79.9
	VII	100.0	92.3	68.1
	VIII	81.4	100.0	72.6
Thoracic	1	39.8	35.2	45.5
	II	21.8	18.4	24.7
	III	14.1	19.1	17.2
	IV	14.1	17.6	13.2
	V	15.3	13 3	14.1
	VI	24.5	11.5	13.6
	VII	24.5	19.1	13.2
	VIII	24.5	13.7	15.7
	IX	23.0	13.1	15.4
	X	25.3	16.8	14.8
	XI	26.0	17.8	17.9
	XII	24.5	24.4	15.9
Lumbar	I	36.9	34.2	22.1
	II	33.5	43.4	27.1
	III	39.8	49.5	46.5
	IV	56.5	57.3	63.2
	V	63.6	62.6	61.4
Sacral	I	100.0	67.3	71.7
	II	56.5	37.5	100.0
	III	16.4	23.0	45.5
	IV	6.7	7.8	22.4
	V	3.2	2.5	8.5
Coc	I	.5	.6	1.9

IV. Determination of the Number of Nerve Fibers in the Dorsal Roots of the Spinal Nerves of Man.

The further significance of the areas of the cross-sections of the dorsal roots can only be fully appreciated when the number of fibers which these roots contain has been determined. As before mentioned, there is, up to the present time, on record

only one attempt at a determination of this kind, viz., that of STILLING.

1. Stilling's Estimate. The material used by STILLING (1859)[15] for this work was the same as that employed in measuring the areas. In this investigation he made use of a compound microscope in the oculus of which was placed an ocular micrometer on which was a square 3‴ (Paris lines) on each side, and each side again was divided into 120 parts by parallel rulings. He counted in a certain number of the small squares thus formed the number of cross-sectioned nerve fibers seen within them, and from this estimated the number for the entire square. This he found to be from 120–176, average 148, for the dorsal roots. He does not state what roots he examined nor how many counts were made. Since the magnification used was 37.5 diameters or 1406 in area, the amount of the section seen within the square would be 9–1406 or 1–156 of a square line. If 1–156 of a square line of the section contains 148 fibers, one square line will contain 156×148, or 23,088 fibers, which is equal to 4,537 fibers for each sq. mm. Since in his case there were 57.95 mm.^{2} in the area of the dorsal roots of the 31 left spinal nerves, there will be 57.95×4,537, or 262,919 nerve fibers in all of them. And since the right dorsal roots have an area of 55.09 mm.^{2}, they will have 55.09×4,537, or 249,943 nerve fibers, and the dorsal roots of both sides 512,862.

STILLING'S estimate for the number of nerve fibers in the dorsal roots of both sides is, however, not 512,862, but 504,473. This difference is due to the fact that he based his estimate on the area of the dorsal roots as obtained by his method of weighing, which gave 111.23 mm.^{2} for both sides, and the calculations I have made are based on his areas as obtained by the planimeter, which gives 113.04 mm.^{2} The latter areas were selected because they may be more properly compared with my own, which were also obtained by planimetric measurements.

2. Author's Enumeration. In making the enumeration of the number of nerve fibers in the dorsal roots of the left spinal

nerves of man, I made use of the same material as was employed in determining the areas of the cross-sections of these roots. The fascicles in the projections used for determining the areas, as is shown in Figs. 2-32, were numbered. Photographs of some 200 diameters enlargement were made from small negatives of the cross-sections of the roots, and in these the fascicles were numbered as in the projections; in addition the sub-divisions of the fascicles were lettered. These subdivisions were not made into individual fascicles, because the septa between them were not sufficiently well developed to warrant it. Both the projections and the photographs were placed on the table in front of the microscope and used in identifying the fascicles the fibers of which I wished to count.

The sections were well stained and the fibers easily recognized in all but a few instances. The characteristic mark sought for in case of doubt is the ring-like appearance of a nerve fiber due to the transparency of its axis-cylinder. In rare cases, however, where a nerve fiber was sectioned through its node of RANVIER this characteristic was not prominent. By means of this characteristic a small nerve fiber is easily distinguished from a connective-tissue corpuscle or a fragment of the medullary sheath. Some difficulty was found in the obliquely sectioned fascicles because the axis-cylinder in such cases was not easily recognized. The amount of connective tissue in some of the thoracic roots was also a source of difficulty in that it made the sections denser by filling up the spaces between the nerve fibers, and thus tended to obscure the small fibers. It is not thought, however, that any important errors have been made as the result of the difficulties named.

In counting, a ZEISS microscope fitted with a mechanical stage, a ZEISS objective, 4 mm., aperture 0.95, and oculus No. 6 or 8, was used. Oculus No. 6 was used only in a few instances where a coarse-fibered fascicle or one of its sub-divisions was too large for the field of vision in a No. 8 oculus, but not too large for that in an oculus No. 6.

In the oculus was placed an ocular micrometer ruled into square millimeters. The cross-sectioned nerve fibers seen with-

in the upper left-hand square were always counted first, then, in the same row, the squares to the right of this, and each succeeding row below the first in alternate directions, so as to avoid confusion by passing across the fascicle from the last square in one row to the first in the next row. The counting was done by means of an automatic register, having a counting limit of 999, and worked by the thumb of the right hand. When a sub-division had been counted the number indicated by the register was recorded on a paper which was numbered and lettered to correspond to the photograph of the cross-section of the root counted. The sub-divisions were later added and the totals placed after the number of the fascicles, as is shown in Tables II–XXXII.

When one sub-division was too large to be seen within one field of the ocular net, the method employed (except in a few cases where oculus 6 was used as mentioned above) was to find landmarks in the section and similar ones in the photograph. One of the limiting lines of the ocular micrometer was made to lie across these landmarks, which in most instances were two conspicuous nerve fibers; one on each side of the fascicle. This limiting line was so arranged as to be at right angles to one of the movements of the mechanical stage. After counting the fibers within all the squares on the side of the limiting line within the field of vision, the mechanical stage, carrying the slide with it, was moved by means of its screws, and the opposite limiting line made to run through the same landmarks, and the rest of the sub-division counted. In counting the cross-sectioned nerve fibers crossed by one of the lines of the ocular micrometer only those fibers the axis-cylinders of which were entirely within that side of the line first counted were considered as belonging to that side, while the rest were considered as belonging to the other side of the line and counted when that side was counted. Most of the counting was done by daylight from a north window. Some counting, however, was done by the aid of an incandescent light placed two feet in front of the microscope.

After counting for fifteen or thirty minutes a few minutes

were taken for rest, and after one hour of counting a longer rest was taken. On the average, about two hours a day were devoted to counting, though on several occasions the period was longer.

The number of fibers counted per hour varied greatly. On three or four mornings, under the most favorable conditions, as many as 3,000 fibers were counted per hour. Under ordinary conditions, from 1,000 to 1,500 fibers per hour was the best that could be done. In very many instances less than 500 per hour was found to be a severe task.

In estimating the accuracy of this enumeration, three sources of error have to be considered.

(a) Errors in the identification of the small nerve fibers. This has already been mentioned. The sources of error here are that either connective tissue corpuscles, or that fragments of broken medullary sheaths may be mistaken for nerve fibers. The characteristic sought for in doubtful cases of this kind is the ring-like appearance of the nerve fiber due to the greater transparency of its axis-cylinder. The only case where this test is not conclusive is where the fiber is cut so obliquely as to fail to show this ring-like aspect. But in these cases the elongated appearance of the fiber is quite different from the appearance of a connective tissue corpuscle and markedly different from the sharp-angled fragments of broken medullary sheaths. Since in only a comparatively few instances are the fibers either cut obliquely or broken into fragments, I consider this source of error very small.

(b) Errors in counting, due to the overlooking of some fibers, or to counting the same fibers twice. To determine the amount of this error I counted, preparatory to my enumeration, certain fascicles several times and found the results to vary less than 2%. It must be apparent that this error also includes, at least to a large extent, the error from source (a). Still it is probable that the error from this source is a trifle greater than this preparatory test shows, because of greater fatigue at times, and poorer conditions, such as light, at other

times. I do not believe, however, that the error from sources (a) and (b) exceed 2% on the average.

(c) Errors due to the possibility that the smallest fibers were not stained, and consequently not seen. The fact that my count gives a result 60% greater than STILLING'S result seems to me good evidence that the smallest fibers were included. Again, by measurements, I found fibers the diameter

TABLE I c.

Showing the Number of Nerve-Fibers Counted in the Dorsal Roots of the Left Spinal Nerves of Man.

	No. of Spinal Segments	Area of Roots in sq. mm.	Number of Nerve Fibers in Each Root	Number of Nerve Fibers in thousands per sq. mm.
Cervical	I	.13	1808	13.6
	II	2.33	28375	12.2
	III	2.14	27119	12.6
	IV	2.01	27102	13.4
	V	2.82	28204	10.0
	VI	4.65	46549	10.0
	VII	4.72	50278	10.6
	VIII	5.11	50173	9.8
Thoracic	I	1.79	17891	10.0
	II	.97	13432	13.7
	III	.98	11701	11.9
	IV	.90	11375	12.5
	V	.68	8352	12.2
	VI	.59	7155	12.1
	VII	.98	12325	12.5
	VIII	.71	8983	12.6
	IX	.67	8163	12.1
	X	.86	10612	12.3
	XI	.91	11403	12.4
	XII	1.25	14125	11.4
Lumbar	I	1.75	18861	10.8
	II	2.22	23640	10.6
	III	2.53	31328	12.3
	IV	2.93	39653	13.5
	V	3.20	43128	13.4
Sacral	I	3.44	47461	13.8
	II	1.92	25545	13.3
	III	1.18	17322	14.9
	IV	.40	8580	21.3
	V	.13	2223	19.3
Coc.	I	.03	761	16.0
Totals	31	54.93	653,627	11.9

of which was only about 2μ to be quite numerous. I think, therefore, that the smallest medullated fibers are included in my count.

In Tables II–XXXII are to be found the number of nerve fibers for each fascicle, and in Table I^{c} is found the totals for each root.

3. *Comparison of Stilling's Estimate with the author's Enumeration.* On comparing the determination of the number of nerve fibers in the dorsal roots of the spinal nerves made by STILLING with those of the author a wide difference is manifest. According to his estimate there are only 262,919 fibers in these roots on one side, while according to my count there are 653,627. In other words, STILLING's result is 39.9%, or in round numbers 40%, of my results. In searching for the source of this difference I found two significant statements by STILLING (1859)[16]. First, that he finds no nerve fibers of so small a diameter as 2.7–4.5μ, and second, that the nerve fibers range, in diameter, from 7—22μ. It thus seems evident that for the most part STILLING failed to see nerve fibers the diameters of which were much less than 7μ, and in this lies the chief source of the difference between our results. I find, as we have seen, that STILLING's results are about 40% of mine, or in other words, my total, in round numbers, is 60% greater than the results of STILLING. It therefore remains to be determined whether this 60% of difference can be explained by the fibers the diameter of which is less than 7μ—these being the fibers smaller than STILLING's lowest limit.

In searching for data to determine this point I find that ROSENTHAL (1845)[4], BIDDER and VOLKMANN (1842)[17], KÖLLIKER (1850)[18], and DUCHENE (1864)[19], estimate the small fibers in the dorsal roots of the spinal nerves of various vertebrates to range from ⅓–½ of their entire number.

SIEMERLING (1886–1887)[20-21], counted in each dorsal root, mostly on the left side, the nerve fibers seen in 9 mm.^{2} of the ocular micrometer. He found that 670 of the nerve fibers so counted were less than 5μ in diameter, and 536 between 5.3–23.9μ—that is, 55½% are small and 44½% large fibers. In

order to determine, roughly, this relation between the large and small fibers I have counted all the nerve fibers the diameter of which is more than 7μ in the dorsal roots of C. II and Th. VII of the spinal nerves of the left side. According to this count the dorsal root of C. II contains 12,621, and that of Th. VII 4,621 of these large fibers. From Table I[d] it is seen that the former contains in all 28,375, and the latter 12,325 nerve fibers. Calculations based on these data indicate that in the dorsal root of C. II 55.5% of the fibers are *less* than 7μ, and in the dorsal root of Th. VII, 62.4%.

We therefore conclude from the calculations based on the results of STILLING and on my own results, that 55 to 60% of the fibers in the dorsal roots of the spinal nerves are less than 7μ in diameter, i. e., having a smaller diameter than the smallest nerve fiber measured by STILLING. The failure on the part of STILLING to include the fibers the diameters of which are less than 7μ is no doubt the chief source of the difference between STILLING's results and my own.

V. The Number of Nerve Fibers per Square Millimeter of the Cross-Section of the Dorsal Roots of the Spinal Nerves of Man.

According to the data which we have taken from STILLING the dorsal roots of the spinal nerves in man have an area on the left side of 57.95 mm.^{2} and contain 262,919 nerve fibers, or in other words, they contain 4,537 nerve fibers per sq. mm. of the cross-section.

According to my results, the dorsal roots in the case examined have on the left side an area of 54.93 mm.^{2}, and contain 653,385 nerve fibers, or on the average, 11,901 nerve fibers per sq. mm. of the cross-sections of the roots.

This comparison is but another way of showing that STILLING failed to observe the small fibers.

In my projections of the dorsal roots of the left side, as well as in the tables accompanying them, are found the relative number of nerve fibers for each fascicle, expressed in thousands per sq. mm. From a study of these it is evident that the rela-

tive number may vary considerably even in the same root. It follows, in general, that the fascicle having a relatively large number of fibers per sq. mm., other things being equal, contains the fibers of smaller diameter. This holds true in a great number of instances, as can easily be seen from a microscopical examination of these fascicles. Still other factors beside the caliber of the nerve fiber enter in to determine this relative number. One of these factors is the amount of connective tissue present in the fascicles. This varies greatly in the different roots due, perhaps, to the fact that the roots were not sectioned at exactly the same point with regard to the *dura mater*. Thus, the cross-sections of the thoracic roots show far more connective tissue than the cervical and lumbar roots. This, no doubt, is one reason why the lumbar roots, although they have a great number of large fibers, yet show such a large number of fibers per sq. mm. On the other hand, this is most probably also the reason why the thoracic roots, which contain many small fibers yet do not show a higher relative number per sq. mm.

Another factor is the compactness of the tissue of the fascicles. That this is often determined by the connective tissue is evident; still in many cases the fibers may be seen to be much scattered without the presence of much connective tissue between them.

Upon studying my results in order to determine whether there be any relation between the diameter of the fascicle and its number of nerve fibers per sq. mm., although no conclusive statement can be made respecting this point, yet it can be said, that in general the small fascicles have fibers of a small caliber.

On the basis of the results obtained by the measurement of the roots and the enumeration of its fibers I have constructed Chart III in Fig. 1. This has been constructed in the same manner as Chart II. The percentage values for these curves are found in Table I^{d} and the figures on which these values are based in Table I^{e}.

TABLE Id.

Giving the Percentage Values of the Areas of the Cross-Sections of the Dorsal Roots of the Spinal Nerves as Compared with the Percentage Distribution of the Number of Medullated Nerve Fibers in Each Dorsal Root. The Greatest Value in each Series is taken as 100%.

	Number of Segments	Percentage Value. (Ingbert) Male	
		Areas	Number of Fibers
Cervical	I	3.6	2.5
	II	56.4	45.6
	III	53.9	41.8
	IV	53.9	39.3
	V	56.0	55.1
	VI	92.5	90.9
	VII	100.0	92.3
	VIII	99.7	100.0
Thoracic	I	35.6	35.2
	II	26.7	18.4
	III	23.2	19.1
	IV	22.6	17.6
	V	16.6	13.3
	VI	14.2	11.5
	VII	24.5	19 1
	VIII	17.6	13.7
	IX	16.2	13.1
	X	21.1	16.8
	XI	22.6	17.8
	XII	28.0	24.4
Lumbar	I	37.5	34.2
	II	47.0	43.4
	III	62.3	49.5
	IV	78.8	57.3
	V	85.7	62.6
Sacral	I	94.3	67.3
	II	50.8	37.5
	III	34.4	23.0
	IV	17.0	7.8
	V	4.4	2.5
Coc.	I	1.0	.6

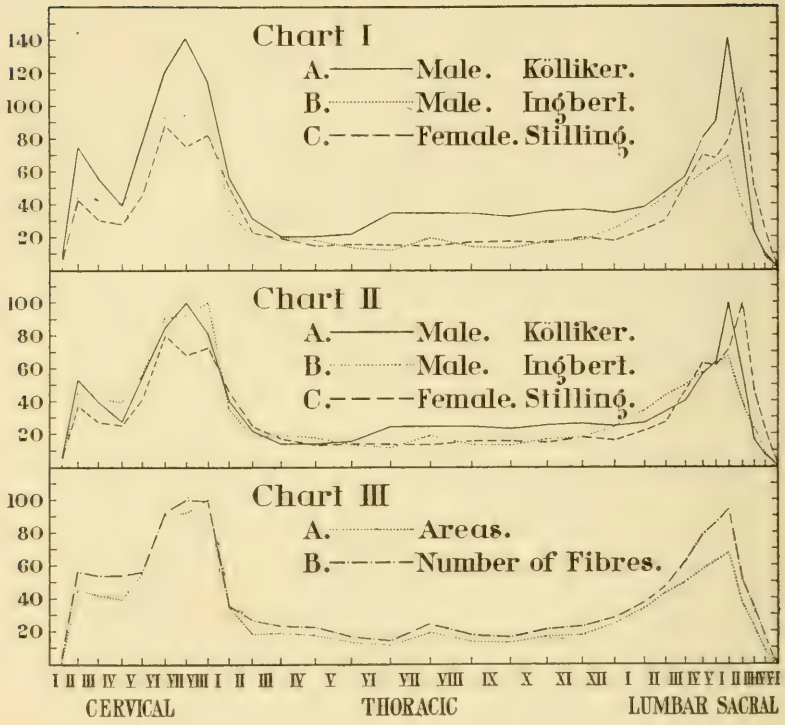


Fig. 1

Chart I. Curves showing the areas in sq. mm. of the cross-sections of the dorsal roots of the left spinal nerves. Each sq. mm. is represented by 20 divisions on the axis of ordinates.

Chart II. Curves based on the measurements used in Chart I; the values in each curve being entered in percentages of the greatest area, which is taken as 100%. One mm. on the axis of ordinates equals 1%.

Chart III. Curves showing in percent. the areas of the cross-sections of the dorsal roots of the left spinal nerves (Author), and the percentage distribution of the number of medullated nerve fibers in each dorsal root. (Author). The close concordance between these two curves is a matter of interest as well as of importance, as it shows that there is a close relation between the size of a root and the number of nerve fibers in it. The divergence in the Lumbar region I take to be due to the compactness of these roots at the places where they were sectioned.

The depression in the curve above C. IV is also a fact worth noticing, whatever may be its significance.

VI. The Classes of Nerve Fibers in the Dorsal Roots of the Spinal Nerves of Man.

That the dorsal roots of mammals are pathways for afferent nerve impulses has been considered as demonstrated since the time of BELL (1811)[22]. This fact has been so often confirmed in man as the result of injury and disease as to need no further discussion. But whether the dorsal roots of man contain efferent nerve fibers in addition to the afferent, is yet an open question. The histological studies of v. LENHOSSÉK (1890)[23], CAJAL (1890)[24] and (1893)[25], VAN GEHUCHTEN (1893)[26], RETZIUS (1892)[27], and MARTIN (1895)[28], have demonstrated in the chick the existence of neurones, the cell bodies of which are located in the spinal cord and the axones of which pass out of the cord by the dorsal roots. It is inferred that these neurones are efferent, but the demonstration of this is still lacking.

By physiological experiments STEINACH (1893 and 1898)[29-30], STEINACH and WIENER (1895)[31] and HORTON SMITH (1897)[32] have demonstrated the presence of efferent fibers in the dorsal roots of the frog.

The degeneration method has given contradictory results. According to VEJAS (1883)[33] and JOSEPH (1887)[34], this method demonstrates in the cat and the rabbit the presence of fibers which degenerate towards the ganglion after section of the dorsal root, while by the same method KAHLER (1884)[35], SINGER and MÜNZER (1890)[36], SHERRINGTON (1894)[37] and (1897)[38], VAN GEHUCHTEN (1895)[39], and GABRI (1896)[40] found no evidence of such fibers in the cat, dog, or monkey.

STRICKER (1876)[41], BONUZZI (1885 and 1887)[42-43], GÄRTNER (1889)[44], MORAT (1892)[45], HASTERLIK and BIEDL (1893)[46], WERZILOFF (1896)[47], and BAYLISS (1900 and 1902)[48-49] have demonstrated by physiological methods vaso-dilator fibers in the dorsal roots of the spinal nerves of the dog. ROUX (1900)[50] in man in cases of tabes reports the demonstration of degenerated nerve fibers of a small caliber in the *rami communicantes*. In order to determine the location of the trophic centres of these fibers ROUX sectioned in the cat the dorsal roots of sev-

eral thoracic nerves and found this to cause a degeneration of small fibers in the sympathetic trunk. He therefore concludes that the cell bodies of these neurones are located in the spinal cord. It is thus evident that as regards man we have not yet any satisfactory demonstration of efferent nerve fibers in the dorsal roots, although their existence seems possible.

VII. The Relation of the Number of Nerve Fibers Proximal and Distal to the Spinal Ganglia.

On this problem we have yet no data for man. SHERRINGTON (1894-5)[51] and others make the statement that in mammals a medullated nerve fiber in the periphery branches little or not at all except near its termination. HARDESTY (1899 and 1900)[52-53], and others have shown that in the frog the number of nerve fibers distal to the spinal ganglia is greater than the number in the dorsal and ventral roots combined. According to DUNN (1900)[54], in the frog about 6 to 8% of all the fibers in the mixed nerves which innervate the thigh divide; and according to her results on the frog, published in 1902[55], in the mixed nerves, about 9-10% of the fibers to the thigh and about 21-22% of the fibers in the shank divide. That nerve fibers may divide at places where the nerve trunk gives off no branches is also demonstrated by her work.

For our calculations, however, it is immaterial whether or not an afferent fiber branches, because the relation which we shall try to establish is one between the area of the dermal surface and the nerve fibers at a place where they are *least* numerous, i. e., in the dorsal roots. Even if there should be a distal excess due to some other cause than distal branching, and even if the fibers which form such an excess should be pathways for afferent impulses, yet the dorsal roots would still constitute the only pathway by means of which these afferent impulses could reach the spinal cord.

VIII. The Application of the Numerical Results to the Innervation of the Skin.

The author had hoped at this time to publish his estimate of the innervation of the dermal surface of the human body based on the enumeration here made. In making such an estimate the number of afferent fibers innervating the skin and the muscles respectively was calculated by the aid of results obtained by STILLING and VOISCHVILLO. But since this part of the thesis was written the author has commenced an enumeration of the number of nerve fibers in the ventral roots of the spinal nerves of man. This investigation as far as carried out shows that the relation of the number of nerve fibers in the dorsal and the ventral roots as given by STILLING is not sufficiently accurate for an estimate of the innervation of the skin. The publication of this part of this investigation will therefore be deferred until the number of nerve fibers in the ventral roots of the spinal nerves of man has been determined, thus presenting proper data for calculating the percent of the dorsal root fibers which innervate the skin and the muscles respectively.

IX. Summary.

1. The total area of the cross-sections of the dorsal roots of the left spinal nerves of a large man is 54.93 mm.^{2}

2. The total number of medullated nerve fibers in the dorsal roots of the left spinal nerves of the same man is 653,627; and the total number on both sides would therefore be about 1,307,254. The error in this instance is probably less than 2%.

3. There are, on the average, 11,900 medullated nerve fibers to every sq. mm. of the cross-sections of the dorsal roots of man.

4. There is a close relation between the area of the cross-sections of the dorsal roots and the number of nerve fibers which they contain. (See Chart III, Fig. 1.)

5. The small fascicles of a dorsal spinal root, in general, contain nerve fibers of small caliber.

6. The number of nerve fibers per sq. mm. of the cross-sections may vary considerably in the different fascicles of the same dorsal spinal root.

In the following Figures (2-32) are given the projections of the dorsal roots of the spinal nerves of man. Their magnification is 34 diameters. Within the outlines of each fascicle are found two numbers; the first designating the number of the fascicle, and the second the number, in thousands, of the nerve fibers per sq. mm. of its cross-section. Thus in C.I there is but one fascicle and this has 13.6 thousands or 13,600 nerve fibers per sq. mm. of its cross-section. In a few of the outlines of the fascicles is found the letter "c." This is to signify that the fascicle was found to be cut obliquely, and that the number indicating the nerves per sq. mm. is that of some neighboring fascicle, and that the corrected area of this fascicle was obtained by dividing the number of fibers in the fascicle by this number of fibers per sq. mm. The outlines are always those of the uncorrected projections. In the Tables (II–XXXII) accompanying the projections are found the data for each root. These tables have four columns of figures; in the first, is found the number given to each fascicle; in the second, the area in sq. mm. of the cross-section of each fascicle; in the third, the number of nerve fibers counted in the cross-section of each fascicle; and in the fourth, the number, in thousands, of nerve fibers per sq. mm. of the cross-section of each fascicle. In cases where a fascicle was found to have been cut obliquely, and its area has been corrected, the number indicating the corrected area is placed in the column itself (the second) and the number indicating the uncorrected area after it in parenthesis. At the bottom of the table are found the totals. These totals have been brought together in Table I^{c}.

TABLES AND FIGURES.

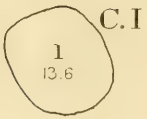

C. I
1
13.6

Fig. 2

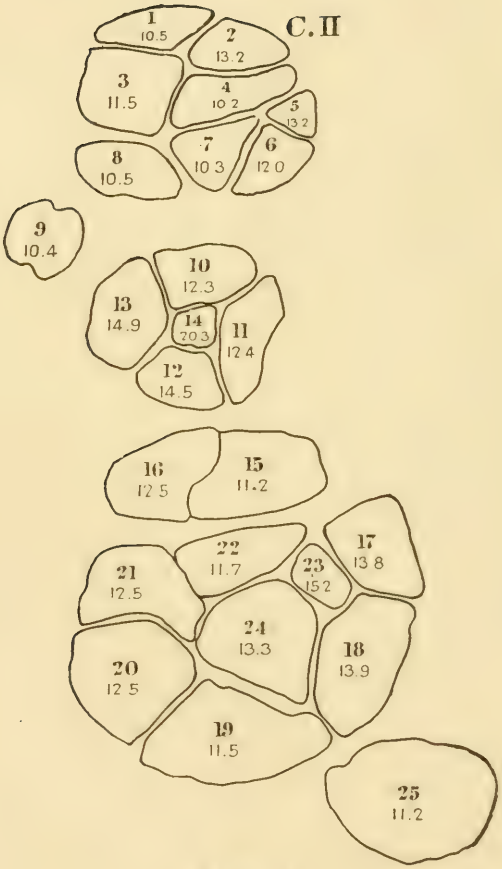

C. II
1
10.5
2
13.2
3
11.5
4
10.2
5
13.2
6
12.0
7
10.3
8
10.5
9
10.4
10
12.3
13
14.9
14
20.3
11
12.4
12
14.5
16
12.5
15
11.2
17
13.8
22
11.7
23
15.2
21
12.5
24
13.3
18
13.9
20
12.5
19
11.5
25
11.2

Fig. 3

TABLE II. C. I.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	0.13	1.808	13.6

TABLE III. C. II.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0528	558	10.5
2	.0549	728	13.2
3	.1076	1241	11.5
4	.0692	707	10.2
5	.0153	222	13.2
6	.0397	479	12.0
7	.0529	548	10.3
8	.0715	749	10.5
9	.0716	744	10.4
10	.0743	913	12.3
11	.0755	941	12.4
12	.0555	807	14.5
13	.0870	1299	14.9
14	.0157	319	20.3
15	.1410	1589	11.2
16	.1047	1315	12.5
17	.0926	1271	13.8
18	.1349	1876	13.9
19	.1926	2221	11.5
20	.1641	2055	12.5
21	.1202	1596	12.5
22	.0884	1036	11.7
23	.0366	557	15.2
24	.1636	1854	13.3
25	.2452	2750	11.2
Totals, 25	2.3274	28,375	12.2 average

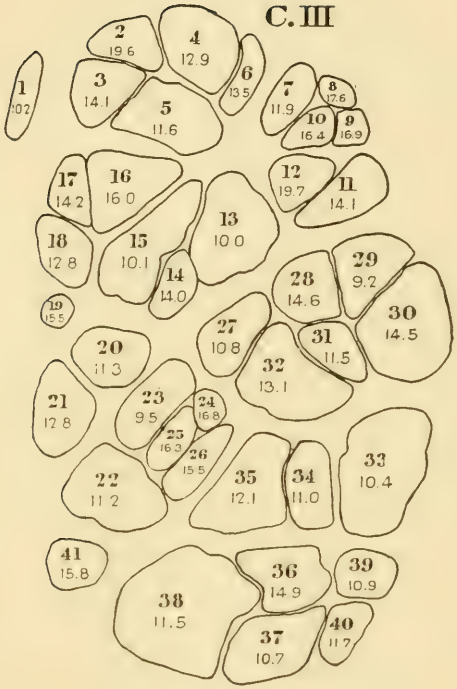

C. III
1 10.2
2 19.6
3 14.1
4 12.9
5 11.6
6 13.5
7 11.9
8 17.6
9 16.9
10 16.4
11 14.1
12 19.7
13 10.0
14 14.0
15 10.1
16 16.0
17 14.2
18 12.8
19 15.5
20 11.3
21 12.8
22 11.2
23 9.5
24 16.8
25 16.3
26 15.5
27 10.8
28 14.6
29 9.2
30 14.5
31 11.5
32 13.1
33 10.4
34 11.0
35 12.1
36 14.9
37 10.7
38 11.5
39 10.9
40 11.7
41 15.8

Fig. 4

TABLE IV. C. III.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0268	276	10.2
2	.0302	592	19.6
3	.0478	673	14.1
4	.0786	1018	12.9
5	.0782	910	11.6
6	.0254	345	13.5
7	.0303	460	11.9
8	.0112	197	17.6
9	.0155	262	16.9
10	.0229	397	16.4
11	.0438	615	14.1
12	.0257	508	19.7
13	.0848	855	10.0
14	.0252	356	14.0
15	.0990	1005	10.1
16	.0612	980	16.0
17	.0308	438	14.2
18	.0415	534	12.8
19	.0118	183	15.5
20	.0521	592	11.3
21	.0644	826	12.8
22	.0940	1054	11.2
23	.0574	549	9.5
24	.0128	215	16.8
25	.0189	309	16.3
26	.0267	416	15.5
27	.0556	601	10.8
28	.0446	652	14.6
29	.0530	488	9.2
30	.1066	1551	14.5
31	.0220	396	19.5
32	.0777	1021	13.1
33	.1236	1288	10.4
34	.0518	570	11.0
35	.1008	1215	12.1
36	.0498	743	14.9
37	.0781	837	10.7
38	.1800	2077	11.5
39	.0355	386	10.9
40	.0286	335	11.7
41	.0249	394	15.8
Totals 41	2,1396	27,119	12.6 average

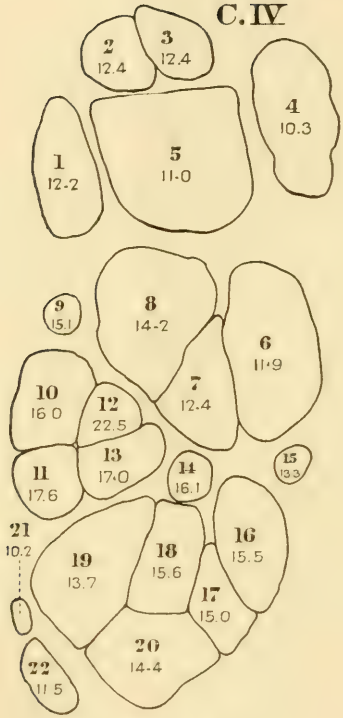

C.IV
2
12.4
3
12.4
4
10.3
1
12-2
5
11-0
9
15.1
8
14-2
6
11·9
10
16 0
12
22.5
7
12.4
11
17.6
13
17·0
14
16.1
15
13.3
21
10.2
19
13.7
18
15.6
16
15.5
17
15.0
20
14-4
22
11 5

Fig. 5

TABLE V. C. IV.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.1090	1335	12.2
2	.0526	654	12.4
3	.0555	691	12.4
4	.1580	1627	10.3
5	.2869	3158	11.0
6	.1810	2166	11.9
7	.0994	1237	12.4
8	.2011	2868	14.2
9	.0187	282	15.1
10	.0909	1458	16.0
11	.0532	937	17.6
12	.0304	685	22.5
13	.0528	997	17.0
14	.0273	439	16.1
15	.0153	204	13.3
16	.1043	1625	15.5
17	.0598	897	15.0
18	.0972	1518	15.6
19	.1615	2225	13.7
20	.1081	1560	14.4
21	.0078	79	10.2
22	.0398	460	11.5
Totals 22	2.0106	27,102	13.4 average

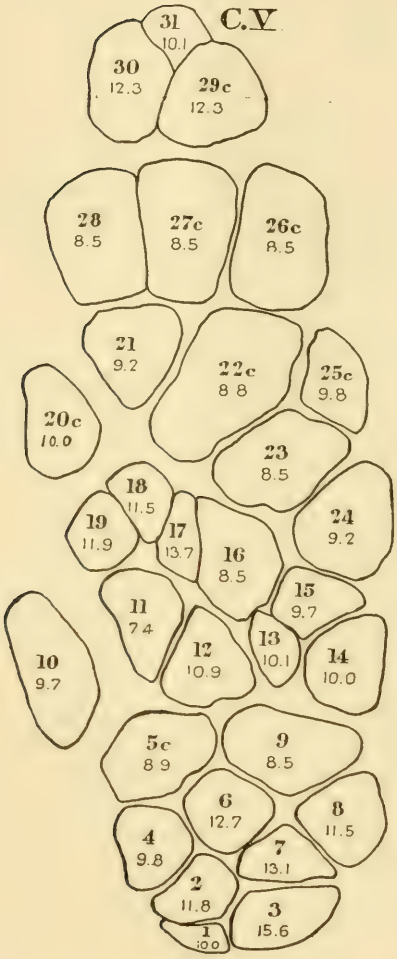

C.V
31
10.1
30
12.3
29c
12.3
28
8.5
27c
8.5
26c
8.5
21
9.2
22c
8 8
25c
9.8
20c
10.0
23
8.5
18
11.5
19
11.9
17
13.7
16
8.5
24
9.2
15
9.7
11
7 4
13
10.1
10
9.7
12
10.9
14
10.0
5c
8 9
9
8.5
6
12.7
8
11.5
4
9.8
7
13.1
2
11.8
3
15.6
1
10.0

Fig. 6

TABLE VI. C.V.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0194	214	11.0
2	.0608	721	11.8
3	.0837	1311	15.6
4	.0837	825	9.8
5	.1144 (.1217)	1017	8.9
6	.0821	1050	12.7
7	.0613	803	13.1
8	.0956	1099	11.5
9	.1364	1169	8.5
10	.1388	1349	9.7
11	.0821	611	7.4
12	.0754	822	10.9
13	.0316	321	10.1
14	.0871	872	10.0
15	.0550	499	9.7
16	.1058	901	8.5
17	.0259	345	13.7
18	.0357	410	11.5
19	.0381	466	11.9
20	.0998 (.1008)	1006	10.0
21	.1112	1036	9.2
22	.2270 (.2310)	2014	8.8
23	.1425	1218	8.5
24	.1241	1142	9.2
25	.0602 (.0802)	594	9.8
26	.1692 (.1816)	1445	8.5
27	.1265 (.1596)	1075	8.5
28	.1072	1112	8.5
29	.0972 (.1274)	1196	12.3
30	.1081	1229	12.3
31	.0319	332	10.1
Totals 31	2.8180	28,204	10.0 average

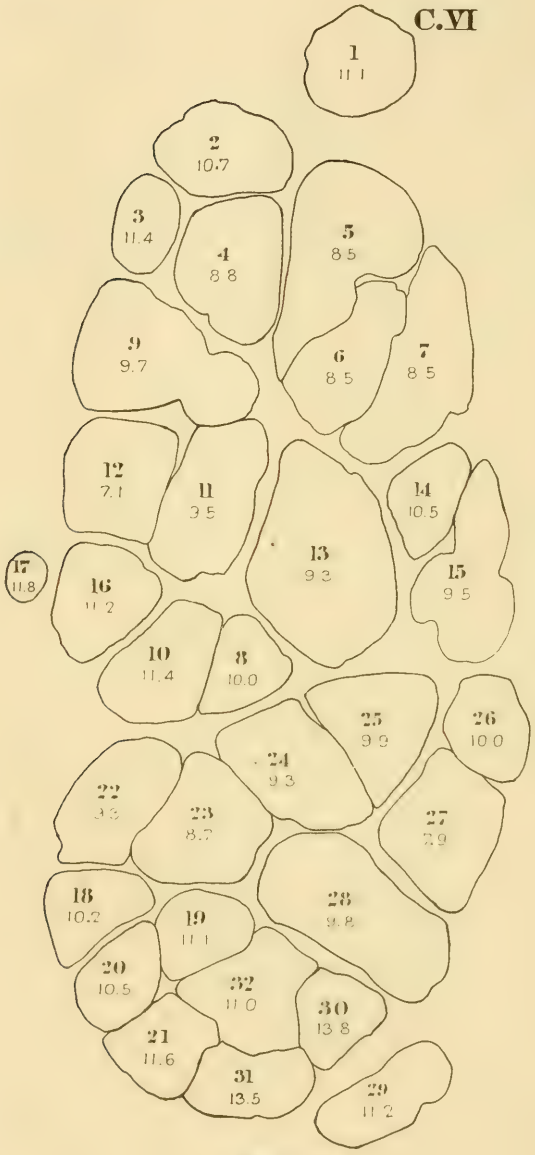

C.VI
1
11.1
2
10.7
3
11.4
4
8.8
5
8.5
6
8.5
7
8.5
9
9.7
12
7.1
11
9.5
14
10.5
13
9.3
15
9.5
17
11.8
16
11.2
10
11.4
8
10.0
25
9.9
26
10.0
24
9.3
22
9.3
23
8.7
27
9.9
18
10.2
19
11.1
28
9.8
20
10.5
32
11.0
30
13.8
21
11.6
31
13.5
29
11.2

Fig. 7

TABLE VII. C.VI.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.1415	1583	11.1
2	.1532	1647	10.7
3	.0782	898	11.4
4	.1956	1724	8.8
5	2717	2327	8.5
6	.1409	1198	8.5
7	.1526	1299	8.5
8	.0937	942	10.0
9	.1957	1911	9.7
10	.1468	1683	11.4
11	.1379	1310	9.5
12	.1675	1365	7.1
13	.3462	3233	9.3
14	.0917	967	10.5
15	.1279	1862	9.5
16	.1046	1181	11.2
17	.0237	280	11.8
18	.1013	1032	10.2
19	.0890	905	11.1
20	.0956	1007	10.5
21	.0944	1103	11.6
22	.1406	1312	9.3
23	.1709	1491	8.7
24	.1791	1770	9.3
25	.1460	1454	9.9
26	.1052	1058	10.0
27	.1992	1391	7.9
28	.2899	2854	9.8
29	.1212	1361	11.2
30	.0840	1165	13.8
31	.1136	1536	13.5
32	.1539	1700	11.0
Totals 32	4.6533	46,549	10.0 average

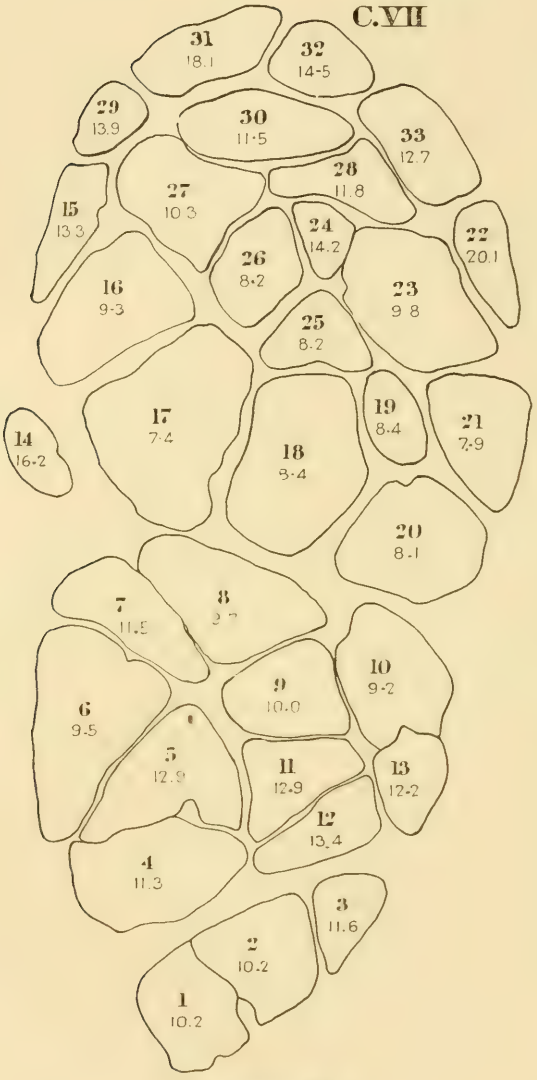

C.VII
31
18.1
32
14·5
29
13.9
30
11·5
33
12.7
28
11.8
27
10.3
15
13.3
24
14.2
22
20.1
26
8·2
16
9·3
23
9·8
25
8.2
17
7·4
19
8.4
21
7·9
14
16·2
18
8·4
20
8.1
7
11.5
8
9·2
10
9·2
9
10.0
6
9·5
5
12.9
11
12.9
13
12·2
12
13.4
4
11.3
3
11.6
2
10.2
1
10.2

Fig. 8

TABLE VIII. C.VII.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0626	639	10.2
2	.1303	1329	10.2
3	.0738	858	11.6
4	.2119	2403	11.3
5	.2045	2656	12.9
6	.2808	2788	9 5
7	.1410	1632	11.5
8	.2115	2052	9.7
9	.1432	1442	10.0
10	.1852	1706	9.2
11	.1197	1536	12.9
12	.1039	1397	13.4
13	.0751	920	12 2
14	.0579	949	16.2
15	.0912	1219	13.3
16	.2111	1962	9.3
17	.3411	2598	7.4
18	.2877	2435	8.4
19	.0681	571	8.4
20	.2077	1684	8.1
21	.1597	1276	7.9
22	.0806	1423	20.1
23	.2477	2439	9.8
24	.0433	628	14.2
25	.0778	638	8.2
26	.1163	953	8.2
27	.1805	1871	10.3
28	.0532	740	11 8
29	.1393	1609	13 9
30	.1014	1852	11.5
31	.0864	1256	18.1
32	.1318	1673	14.5
33	.0970	1144	12.7
Totals 33	4.7233	50,278	10.6 average

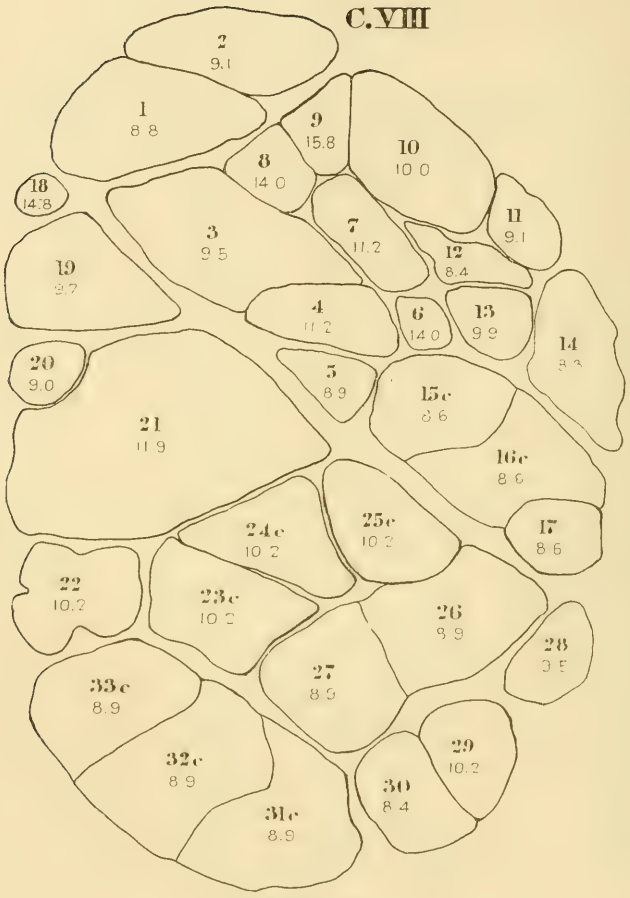
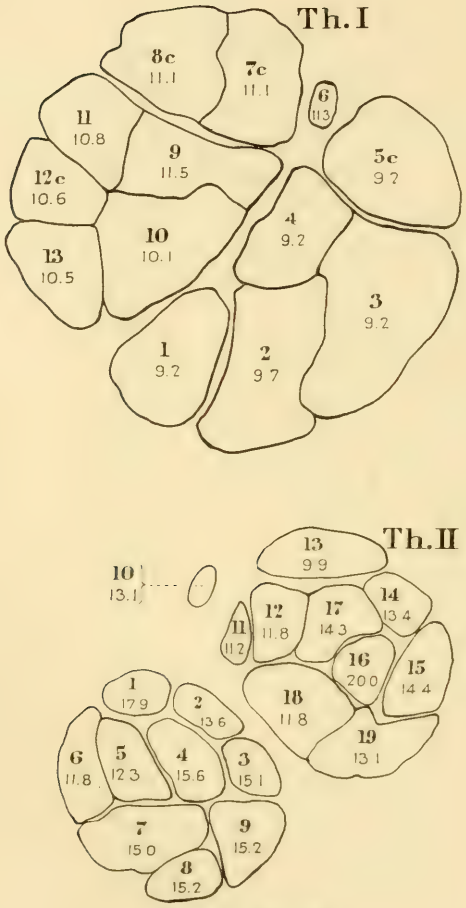

C.VIII
2
9.1
1
8 8
9
15.8
10
10 0
8
14 0
18
14.8
3
9 5
7
11.2
11
9.1
12
8.4
19
9.7
4
11 2
6
14 0
13
9 9
14
20
9.0
5
8 9
15c
8 6
21
11 9
16c
8 6
24c
10 2
25c
10 2
17
8 6
22
10.2
23c
10 2
26
9 9
28
9 5
33c
8.9
27
8 9
32c
8 9
29
10.2
30
8 4
31c
8.9

Fig. 9

TABLE IX. C.VIII.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.2573	2231	8.8
2	.1736	1586	9.1
3	.3133	2993	9.5
4	.1176	1322	11.2
5	.0680	601	8.9
6	.0226	331	14.0
7	.1135	1274	11.2
8	.0569	802	14.0
9	.0501	791	15.8
10	.2312	2323	10.0
11	.0733	673	9.1
12	.0612	515	8.4
13	.0721	714	9.9
14	.1797	1495	8.3
15	.1582 (.1710)	1361	8.6
16	.1527 (.2140)	1314	8.6
17	.0838	722	8.6
18	.0241	360	14.8
19	.2091	1897	9.7
20	.0452	409	9.0
21	.7007	8395	11.9
22	.1659	1694	10.2
23	.1695 (.2096)	1637	10.2
24	.1399 (.1718)	1366	10.2
25	.1642 (.1675)	1490	10.2
26	.2511	2237	8.9
27	.1961	1764	8.9
28	.0915	878	9.5
29	.1059	1082	10.2
30	.1254	1062	8.4
31	.1356 (.2732)	1206	8.9
32	.2578 (.2886)	2395	8.9
33	.1408 (.2262)	1253	8.9
Totals 33	5,1078	50,173	9,8 average


Th. I
8c
11.1
7c
11.1
6
11.3
11
10.8
9
11.5
5c
9.7
12c
10.6
4
9.2
10
10.1
13
10.5
3
9.2
1
9.2
2
9.7
Th. II
13
9.9
10
13.1
12
11.8
17
14.3
14
13.4
11
11.2
16
20.0
15
14.4
1
17.9
2
13.6
18
11.8
19
13.1
6
11.8
5
12.3
4
15.6
3
15.1
7
15.0
9
15.2
8
15.2

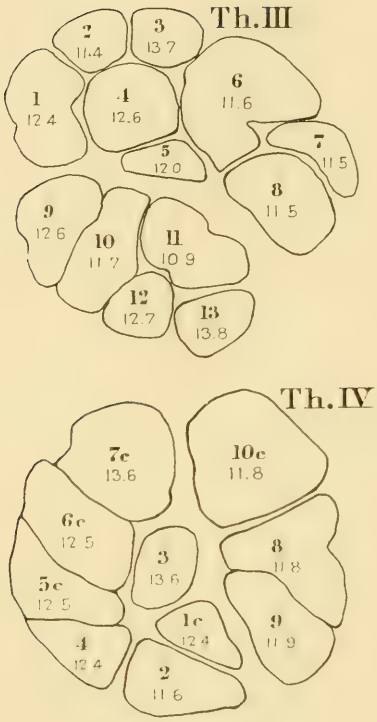
Figs. 10, 11

TABLE X. Th. I.

Number of Fascicle		Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
	1	.1579	1455	9.2
	2	.2267	2208	9.7
	3	.2895	2653	9.2
	4	.1155	1063	9.2
	5	.1778 (.1888)	1627	9.2
	6	.0133	151	11.3
	7	.1234 (.1497)	1370	11.1
	8	.1271 (.1459)	1411	11.1
	9	.1131	1311	11.5
	10	.1744	1762	10.1
	11	.0964	1045	10.8
	12	.0729 (.0791)	773	10.6
	13	.1010	1062	10.5
Totals	13	1.7890	17,891	10.0 average

TABLE XI. Th. II.

Number of Fascicle		Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq mm.
	1	.0311	569	17.9
	2	.0307	418	13.6
	3	.0334	505	15.1
	4	.0569	899	15.6
	5	.0584	721	12.3
	6	.0627	741	11.8
	7	.0878	1317	15.0
	8	.0384	585	15.2
	9	.0670	1035	15.2
	10	.0067	88	13.1
	11	.0207	232	11.2
	12	.0512	608	11.8
	13	.0720	713	9.9
	14	.0379	510	13.4
	15	.0595	848	14.4
	16	.0331	662	20.0
	17	.0509	731	14.3
	18	.0994	1181	11.8
	19	.0815	1069	13.1
Totals	19	.9742	13,432	13.7 average


Th.III
2
11.4
3
13.7
1
12.4
4
12.6
6
11.6
5
12.0
7
11.5
8
11.5
9
12.6
10
11.7
11
10.9
12
12.7
13
13.8
Th.IV
7c
13.6
10c
11.8
6c
12.5
3
13.6
8
11.8
5c
12.5
1c
12.4
9
11.9
4
12.4
2
11.6

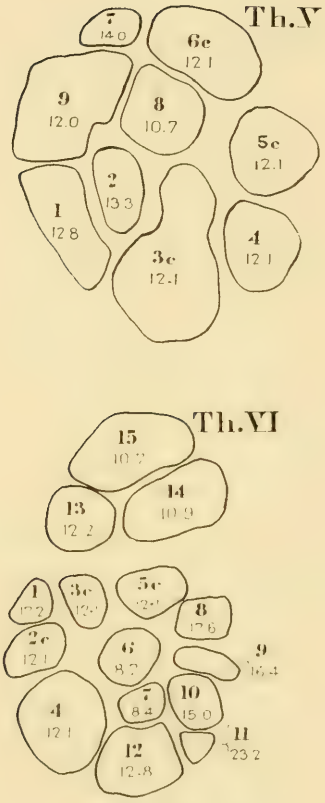
Figs. 12, 13

TABLE XII. Th. III.

Number of Fascicle	Area of Fascicles in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0876	1094	12.4
2	.0466	532	11.4
3	.0448	614	13.7
4	.0905	1142	12.6
5	.0373	447	12.0
6	.1672	1946	11.6
7	.0536	617	11.5
8	.1078	1236	11.5
9	.0767	867	12.6
10	.0841	989	11.7
11	.0984	1082	10.9
12	.0378	479	12.7
13	.0472	656	13.8
Totals 13	.9796	11,701	11.9 average

TABLE XIII. Th. IV.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0487 (.0543)	605	12.4
2	.0922	1077	11.6
3	.0584	794	13.6
4	.0563	698	12.4
5	.0753 (.0860)	942	12.5
6	.0984 (.1262)	1231	12.5
7	.1189 (.1425)	1617	13.6
8	.1276	1512	11.8
9	.0992	1191	11.9
10	.1281	1708	11.8
Totals 10	.9031	11,375	12.5 average


Th.V
7
14.0
6c
12.1
9
12.0
8
10.7
5c
12.1
2
13.3
1
12.8
3c
12.1
4
12.1
Th.VI
15
10.2
14
10.9
13
12.2
1
12.2
3c
12.2
5c
12.1
8
12.6
2c
12.1
6
8.2
9
10.4
4
12.1
7
8.4
10
15.0
11
23.2
12
12.8

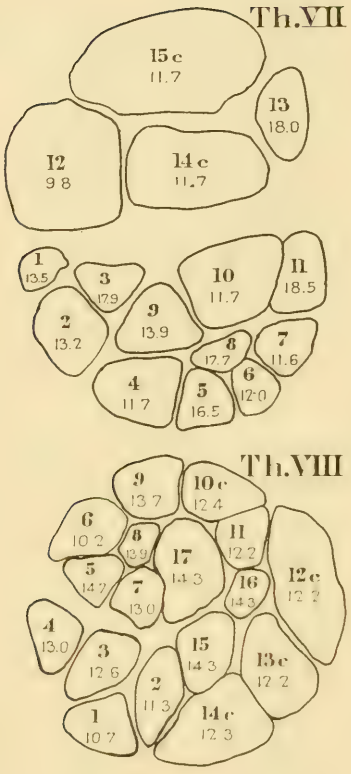
Figs. 14, 15

TABLE XIV. Th. V.

Number of Fascicle		Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
	1	.0926	1198	12.8
	2	.0459	605	13.1
	3	.1272 (.1859)	1539	12.1
	4	.0720	872	12.1
	5	.0556 (.0800)	673	12.1
	6	.0756 (.1020)	916	12.1
	7	.0184	258	14.0
	8	.0657	703	10.7
	9	.1313	1588	12.0
Totals	9	.6843	8352	12.2 average

TABLE XV. Th. VI.

Number of Fascicle		Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
	1	.0144	248	17.2
	2	.0243 (.0305)	294	12.1
	3	.0565 (.0958)	684	12.1
	4	.0201	244	12.1
	5	.0252 (.0359)	306	12.1
	6	.0306	269	8.7
	7	.0173	146	8.4
	8	.0226	402	17.6
	9	.0152	249	16.4
	10	.0288	432	15.0
	11	.0082	191	23.2
	12	.0633	793	12.8
	13	.0439	537	12.2
	14	.0812	888	10.9
	15	.1377	1472	10.7
Totals	15	.5893	7155	12.1 average


Th.VII
15c
11.7
13
18.0
12
9 8
14c
11.7
1
13.5
3
17.9
10
11.7
11
18.5
2
13.2
9
13.9
8
12.7
7
11.6
4
11 7
5
16.5
6
12·0
Th.VIII
9
13 7
10c
12 4
6
10 2
8
12.9
11
12.2
17
14 3
5
14 7
7
13 0
16
14 3
12c
12 2
4
13.0
3
12 6
15
14 3
13c
12 2
2
11 3
1
10 7
14c
12 3

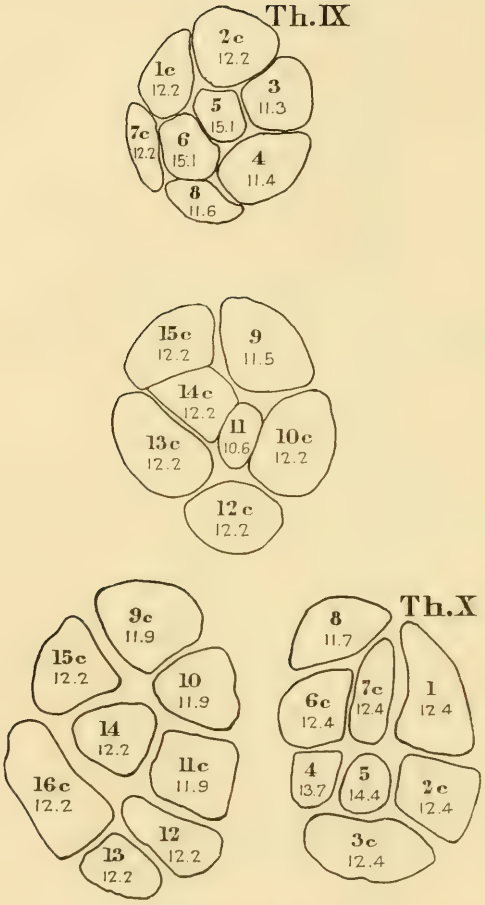
Figs. 16, 17

TABLE XVI. Th. VII.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0154	208	13.5
2	.0549	725	13.2
3	.0268	482	17.9
4	.0645	760	11.7
5	.0325	539	16.5
6	.0253	306	12.0
7	.0339	392	11.6
8	.0161	286	17.7
9	.0536	747	13.9
10	.1073	1265	11.7
11	.0388	718	18.5
12	.1914	1871	9.8
13	.0420	756	18.0
14	.1304 (.1500)	1526	11.7
15	.1490 (.2391)	1744	11.7
Totals 15	.9819	12,325	12.5 average

TABLE XVII. Th. VIII.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0462	497	10.7
2	.0480	548	11.3
3	.0445	561	12.6
4	.0350	458	13.0
5	.0223	330	14.7
6	.0494	507	10.2
7	.0251	327	13.0
8	.0132	183	13.9
9	.0396	542	13.7
10	.0300 (.0458)	373	12.4
11	.0251	307	12 2
12	.0686 (.1304)	837	12 2
13	.0594 (.0825)	726	12.2
14	.0762 (.1047)	937	12.3
15	.0403	577	14.3
16	.0198	285	14.3
17	.0673	988	14.3
Totals 17	.7102	8983	12.6 average


Th.IX
2c 12.2
1c 12.2
3 11.3
5 15.1
7c 12.2
6 15.1
4 11.4
8 11.6
15c 12.2
9 11.5
14c 12.2
11 10.6
13c 12.2
10c 12.2
12c 12.2
9c 11.9
15c 12.2
10 11.9
14 12.2
11c 11.9
16c 12.2
12 12.2
13 12.2
Th.X
8 11.7
6c 12.4
7c 12.4
1 12.4
4 13.7
5 14.4
2c 12.4
3c 12.4

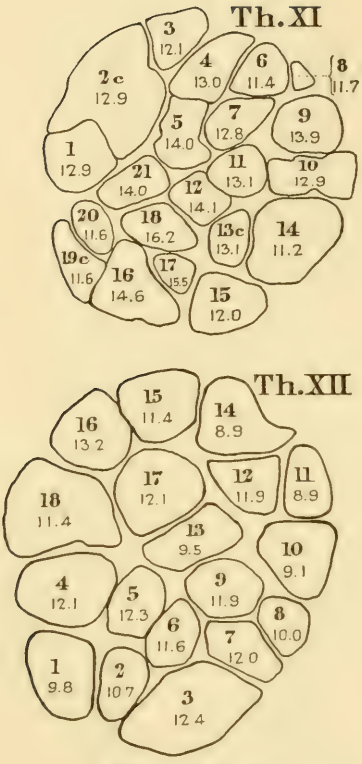
Figs. 18, 19

TABLE XVIII. Th. IX.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0361 (.0494)	441	12.2
2	.0477 (.0684)	573	12.2
3	.0467	528	11.3
4	.0614	702	11.4
5	.0264	399	15.1
6	.0368	555	15.1
7	.0221 (.0348)	280	12.2
8	.0305	355	11.6
9	.0902	1043	11.5
10	.0798 (.0916)	973	12.2
11	.0250	265	10.6
12	.0405 (.0542)	494	12.2
13	.0436 (.1058)	532	12.2
14	.0362 (.0659)	442	12.2
15	.0472 (.0516)	581	12.2
Totals 15	.6702	8163	12.1 average

TABLE XIX. Th. X.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0764	952	12.4
2	.0517 (.0661)	640	12.4
3	.0660 (.0819)	819	12.4
4	.0260	358	13.7
5	.0268	387	14.4
6	.0523 (.0620)	649	12.4
7	.0424 (.0487)	526	12.4
8	.0588	686	11.7
9	.0552 (.0930)	657	11.9
10	.0697	833	11.9
11	.0635 (.0786)	756	11.9
12	.0465	568	12.2
13	.0273 (.0364)	334	12.2
14	.0554	676	12.2
15	.0609 (.0679)	743	12.2
16	.0842 (.1206)	1028	12.2
Totals 16	.8631	10,612	12.3 average


Th.XI
3
12.1
4
13.0
6
11.4
8
11.7
2c
12.9
5
14.0
7
12.8
9
13.9
1
12.9
21
14.0
11
13.1
10
12.9
12
14.1
20
11.6
18
16.2
13c
13.1
14
11.2
19c
11.6
16
14.6
17
15.5
15
12.0
Th.XII
15
11.4
14
8.9
16
13.2
17
12.1
12
11.9
11
8.9
18
11.4
13
9.5
10
9.1
4
12.1
5
12.3
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10.0
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11.6
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12.0
1
9.8
2
10.7
3
12.4

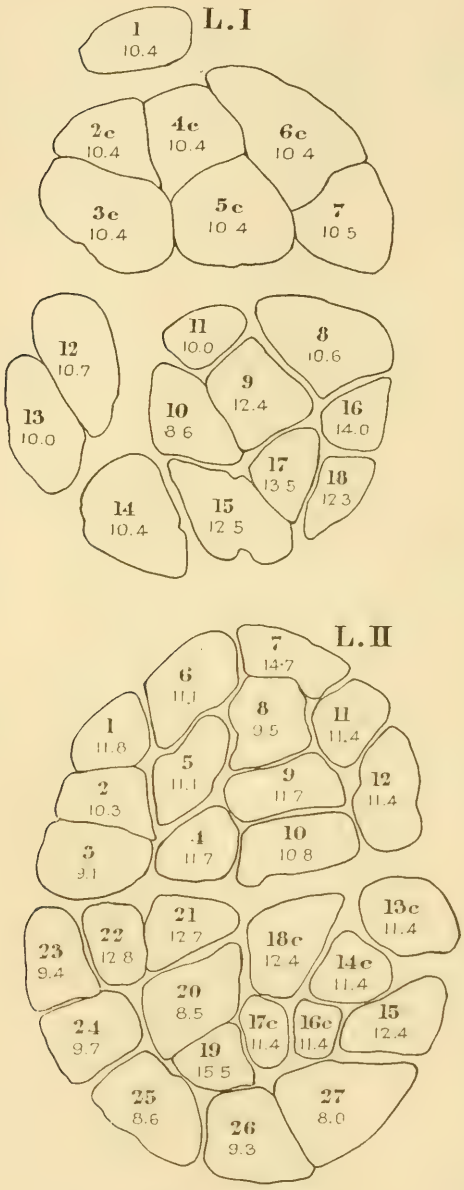
Figs. 20, 21

TABLE XX. Th. XI.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0435	562	12.9
2	.1107 (.1300)	1528	12.9
3	.0393	479	12.1
4	.0346	449	13.0
5	.0368	515	14.0
6	.0321	367	11.4
7	.0367	471	12.8
8	.0069	81	11.7
9	.0474	660	13.9
10	.0483	614	12.9
11	.0323	423	13.1
12	.0283	399	14.1
13	.0193 (.0257)	253	13.1
14	.0981	1109	11.2
15	.0542	651	12.0
16	.0500	731	14.6
17	.0162	256	15.5
18	.0352	571	16.2
19	.0448 (.0560)	510	11.6
20	.0352	304	11.6
21	.0335	470	14.0
Totals, 21	.9134	11,403	12.4 average

TABLE XXI. Th. XII.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0728	719	9.8
2	.0433	466	10.7
3	.1341	1652	12.4
4	.0882	1072	12.1
5	.0492	605	12.3
6	.0416	484	11.6
7	.0495	696	12.0
8	.0333	370	10.9
9	.0578	685	11.9
10	.0717	653	9.1
11	.0481	425	8.9
12	.0542	644	11.9
13	.0619	588	9.5
14	.0744	668	8.9
15	.0734	842	11.4
16	.0710	940	13.2
17	.0926	1125	12.1
18	.1300	1491	11.4
Totals 18	1.2471	14,125	11.4 average


L.I
1
10.4
2c
10.4
4c
10.4
6c
10 4
3c
10.4
5c
10 4
7
10 5
12
10.7
13
10.0
11
10.0
8
10.6
9
12.4
10
8 6
16
14.0
17
13 5
18
12 3
14
10.4
15
12 5
L.II
7
14·7
6
11.1
8
9 5
11
11.4
1
11.8
5
11.1
9
11 7
12
11.4
2
10.3
4
11 7
10
10 8
3
9.1
21
12 7
13c
11.4
22
12 8
23
9.4
18c
12 4
14c
11.4
20
8.5
24
9.7
17c
11.4
16c
11.4
15
12.4
19
15 5
25
8.6
26
9.3
27
8.0

Figs. 22, 23

TABLE XXII. L. I.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0842	876	10.4
2	.0627 (.0745)	652	10.4
3	.1429 (.1602)	1491	10.4
4	.0613 (.0964)	638	10.4
5	.1008 (.1519)	1048	10.4
6	.1570 (.1787)	1633	10.4
7	.1004	1054	10.5
8	.1433	1538	10.6
9	0832	1032	12.4
10	.1135	979	8.6
11	.0546	549	10.0
12	.1172	1252	10.7
13	.1243	1245	10.0
14	.1403	1459	10.4
15	.1071	1350	12.5
16	.0569	695	14.0
17	.0467	656	13.5
18	.0543	714	12.3
Totals 18	1.7507	18,861	10.8 average

TABLE XXIII. L. II.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0509	661	11.8
2	.0775	798	10.3
3	.1053	962	9.1
4	.0718	841	11.7
5	.0787	886	11.1
6	.1026	1146	11.1
7	.0678	997	14.7
8	.1037	984	9.5
9	.0778	915	11.7
10	.0969	1046	10.8
11	.0651	768	11.4
12	.1004	1146	11.4
13	.0838 (.0872)	937	11.4
14	.0513 (.0590)	585	11.4
15	.0873	1089	12.4
16	.0240 (.0338)	274	11.4
17	.0298 (.0397)	338	11.4
18	.1007 (.1036)	1148	12.4
19	.0446	692	15.5
20	.1174	998	8.5
21	.0609	779	12.7
22	.0400	514	12.8
23	.0840	791	9.4
24	.1010	983	9.7
25	.1171	1006	8.6
26	.1055	983	9.3
27	.1713	1373	8.0
Totals 27	2.2172	23,640	10.6 average

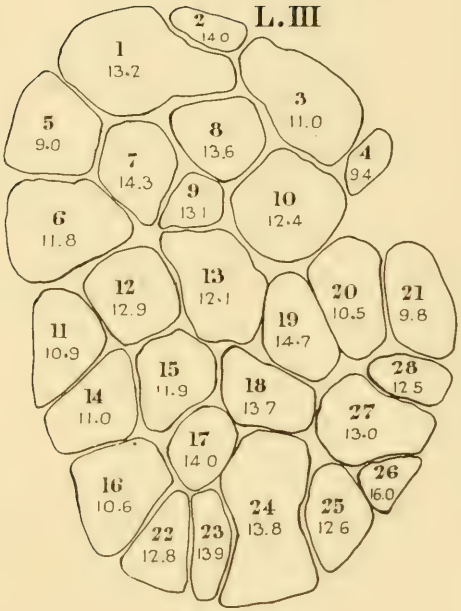

L.III
2
14.0
1
13.2
3
11.0
5
9.0
8
13.6
4
9.4
7
14.3
9
13.1
10
12.4
6
11.8
12
12.9
13
12.1
20
10.5
21
9.8
19
14.7
11
10.9
15
11.9
18
13.7
28
12.5
14
11.0
27
13.0
17
14.0
26
16.0
16
10.6
24
13.8
25
12.6
22
12.8
23
13.9

Fig. 24

TABLE XXIV. L. III.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.1773	2354	13.2
2	.0324	455	14.0
3	.1397	1541	11.0
4	.0301	285	9.4
5	.1133	1023	9.0
6	.1376	1624	11.8
7	.0872	1250	14.3
8	.0841	1146	13.6
9	.0387	509	13.1
10	.1321	1644	12.4
11	.0885	965	10.9
12	.0983	1177	12.9
13	.1304	1584	12.1
14	.0893	987	11.0
15	.0884	1059	11.9
16	.1145	1214	10.6
17	.0566	793	14.0
18	.0848	1162	13.7
19	.0846	1253	14.7
20	.0964	1014	10.5
21	.0958	943	9.8
22	.0622	997	12.8
23	.0519	719	13.9
24	.1767	2446	13 8
25	.0720	910	12.6
26	.0336	538	16.0
27	.0974	1273	13.0
28	.0370	463	12.5
Totals 28	2.5309	31,328	12.3 average

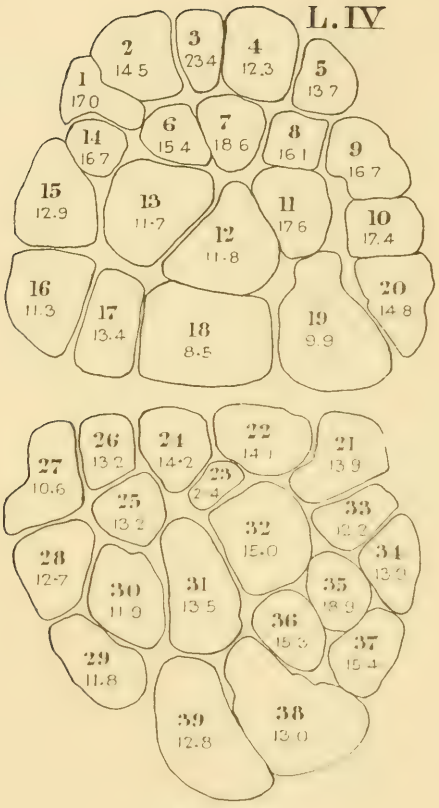

L. IV
1
17·0
2
14·5
3
23·4
4
12·3
5
13·7
6
15·4
7
18·6
8
16·1
9
16·7
10
17·4
11
17·6
12
11·8
13
11·7
14
16·7
15
12·9
16
11·3
17
13·4
18
8·5
19
9·9
20
14·8
21
13·9
22
14·1
23
2·4
24
14·2
25
13·2
26
13·2
27
10·6
28
12·7
29
11·8
30
11·9
31
13·5
32
15·0
33
12·2
34
13·9
35
18·9
36
15·3
37
15·4
38
13·0
39
12·8

Fig. 25

TABLE XXV. L. IV.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0405	707	17.0
2	.0780	1131	14.5
3	.0309	725	23.4
4	.0787	968	12.3
5	.0499	696	13.7
6	.0420	649	15.4
7	.0475	887	18.6
8	.0315	521	16.1
9	.0572	959	16.7
10	.0474	824	17.4
11	.0643	1142	17.6
12	.1102	1311	11.8
13	.1184	1389	11.7
14	.0294	491	16.7
15	.0765	992	12.9
16	.0875	997	11.3
17	.0567	761	13.4
18	.1792	1537	8.5
19	.1523	1517	9.9
20	.0677	993	14.8
21	.0866	1210	13.9
22	.0656	992	14.1
23	.0194	426	21.4
24	.0578	942	14.2
25	.0485	640	13.2
26	.0467	621	13.2
27	.0830	879	10.6
28	.0826	1056	12.7
29	.0770	910	11.8
30	.0843	1007	11.9
31	.1209	1633	13.5
32	.1144	1725	15.0
33	.0485	595	12.2
34	.0577	804	13.9
35	.0505	959	18.9
36	.0564	865	15.3
37	.0690	1063	15.4
38	.1702	2228	13.0
39	.1491	1901	12.8
Totals 39	2,9340	39,653	13.5 average

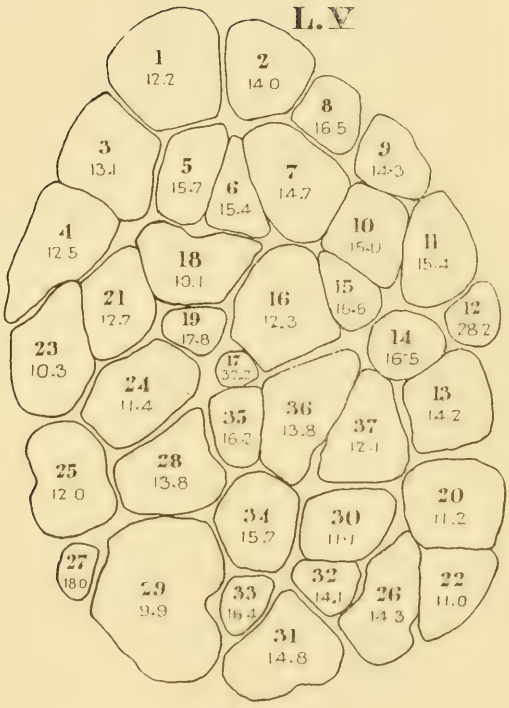

L.V
1
12.2
2
14.0
8
16.5
3
13.1
5
15.7
6
15.4
7
14.7
9
14.3
4
12.5
18
13.1
10
15.0
11
15.4
21
12.7
19
17.8
16
12.3
15
16.6
12
28.2
23
10.3
17
32.2
14
16.5
24
11.4
35
16.2
36
13.8
37
12.1
13
14.2
25
12.0
28
13.8
34
15.7
30
11.1
20
11.2
27
18.0
29
9.9
33
19.4
32
14.1
26
14.3
22
11.0
31
14.8

Fig. 26

TABLE XXVI. L.V.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.1550	1903	12.2
2	.0925	1301	14.0
3	.0976	1280	13.1
4	.1135	1431	12.5
5	.0767	1206	15.7
6	.0542	835	15.4
7	.1139	1681	14.7
8	.0516	852	16.5
9	.0610	875	14.3
10	.0810	1218	15.0
11	.0891	1379	15.4
12	.0257	726	28.2
13	.0895	1273	14.2
14	.0553	914	16.5
15	.0443	739	16.6
16	.1306	1607	12.3
17	.0103	332	32.2
18	.1595	1622	10.1
19	.0125	483	17.8
20	.1138	1280	11.2
21	.0827	1058	12.7
22	.0604	687	11.0
23	.1296	1338	10.3
24	.1305	1504	11.4
25	.1086	1304	12.0
26	.0758	1394	14.3
27	.0181	326	18.0
28	.1050	1467	13.8
29	.2525	2490	9.9
30	.0865	966	11.1
31	.1189	1760	14.8
32	.0346	561	14.1
33	.0233	383	16.4
34	.0869	1368	15.7
35	.0470	763	16.2
36	.1189	1639	13.8
37	.0951	1193	12.1
Totals 37	3,2020	43,128	13.4 average

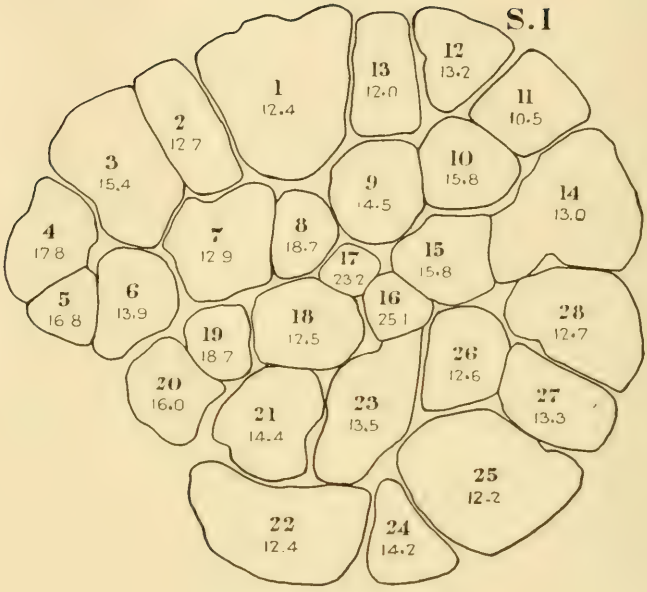
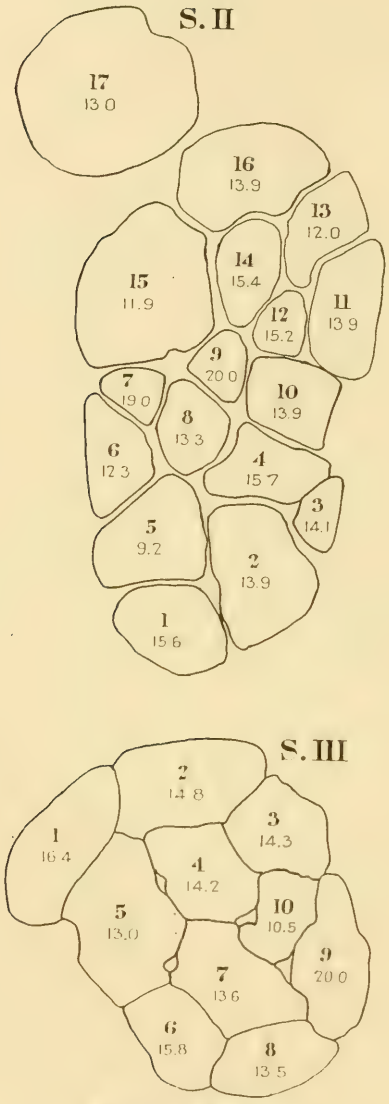

S.I
1
12.4
2
12 7
3
15.4
4
17 8
5
16 8
6
13.9
7
12 9
8
18.7
9
14.5
10
15.8
11
10.5
12
13.2
13
12.0
14
13.0
15
15.8
16
25 1
17
23 2
18
12.5
19
18 7
20
16.0
21
14.4
22
12.4
23
13.5
24
14.2
25
12.2
26
12.6
27
13.3
28
12.7

Fig. 27

TABLE XXVII. S. I.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.2955	3665	12.4
2	.1259	1606	12.7
3	.1824	2816	15.4
4	.0939	1680	17.8
5	.0430	724	16.8
6	.0924	1292	13.9
7	.1423	1839	12.9
8	.0530	993	18.7
9	.1114	1622	14.5
10	.0946	1496	15.8
11	.1266	1331	10.5
12	.0899	1187	13.2
13	.1075	1293	12.0
14	.2292	2980	13.0
15	.0976	1552	15.8
16	.0326	821	25.1
17	.0212	492	23.2
18	.1212	1526	12.5
19	.0499	936	18.7
20	.0908	1461	16.0
21	.1367	1977	14.4
22	.2341	2916	12.4
23	.1540	2079	13.5
24	.0682	1020	14.2
25	.2603	3178	12.2
26	.1011	1279	12.6
27	.1107	1482	13.3
28	.1734	2218	12.7
Totals 28	3.4394	47,461	13.8 average


S. II
17
13.0
16
13.9
13
12.0
14
15.4
15
11.9
12
15.2
11
13.9
9
20.0
7
19.0
10
13.9
8
13.3
6
12.3
4
15.7
3
14.1
5
9.2
2
13.9
1
15.6
S. III
2
14.8
1
16.4
3
14.3
4
14.2
10
10.5
5
13.0
9
20.0
7
13.6
6
15.8
8
13.5

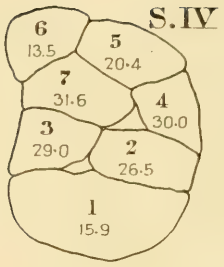
Figs. 28, 29

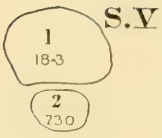
TABLE XXVIII. S. II.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.1135	1524	15.6
2	.1651	2298	13.9
3	.0270	382	14.1
4	.0871	1373	15.7
5	.1356	1251	9.2
6	.0849	1052	12.3
7	.0312	595	19.0
8	.0652	866	13.3
9	.0315	631	20.0
10	.0861	1197	13.9
11	.1189	1652	13 9
12	.0367	559	15.2
13	.0935	1128	12.0
14	.0728	1122	15.4
15	.2592	3079	11.9
16	.1627	2274	13.9
17	.3504	4562	13.0
Totals 17	1.9214	25,545	13.3 average

TABLE XXIX. S. III.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.1231	2027	16.4
2	.1672	2490	14.8
3	.1092	1565	14.3
4	.1099	1568	14.2
5	.1696	2205	13.0
6	.0916	1452	15.8
7	.1333	1815	13.6
8	.1029	1389	13.5
9	.1091	2185	20.0
10	.0594	626	10.5
Totals 10	1.1753	17,322	14.9 average







Figs. 30, 31, 32

TABLE XXX. S. IV.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0588	794	15.9
2	.0488	997	26.5
3	.0366	1101	29.0
4	.0434	1161	30.0
5	.0440	1392	20.4
6	.0330	958	13.5
7	.1368	2177	31.6
Totals 7	.4014	8580	21.3 average

TABLE XXXI. S. V.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0938	1719	18.3
2	.0220	507	23.0
Totals 2	.1258	2226	19.1 average

TABLE XXXII. COC. I.

Number of Fascicle	Area of Fascicle in sq. mm.	Number of Nerve Fibers in Each Fascicle	Number of Nerve Fibers in Thousands per sq. mm.
1	.0324	761	23.5

ERRATA.

Page 54, line 15 from the bottom, for *H. Rosenthal*, read *D. Rosenthal.*

Page 59, lines 11, 12 and 13, for *mm.* read mm^2.

Page 60, line 12 from bottom, for 56.39, read 56.319.

Page 63, line 14 for *Since the magnification used*, read *Since the magnification of the objective used.*

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ON THE PHYLOGENY AND MORPHOLOGICAL POSITION OF THE TERMINAL BUDS OF FISHES.[1]

By C. Judson Herrick.

These curious sense organs occurring in the skin of certain fishes have been a source of perplexity and controversy among morphologists since their discovery by Leydig in 1851. They are found freely scattered over the surface of the skin of the head and trunk in certain teleostean and ganoidean fishes, particularly in exposed situations, and hence by many observers have been regarded as tactile organs. Indeed, Merkel in 1880, having failed altogether to find the proper tactile nerves in the skin of fishes belonging to what we now designate as the general cutaneous system, supposed that these organs, together with the neuromasts or organs of the lateral line system, were developed in compensation for the absence of the typical free tactile nerve endings of the other vertebrates. This we now know to be wide of the mark, for all fishes which possess either or both of the systems of special sense organs mentioned above also possess in the same cutaneous areas an abundant general cutaneous nerve supply for tactile sensation.

We must distinguish at the outset three distinct types of sensory nerve endings in the skin of fishes and then inquire into their respective morphological rank; viz., (1) the general cutaneous nerve termini, (2) the neuromasts, or organs of the acustico-lateralis system of sense organs, (3) the terminal buds, or end-buds.

(1) The first type comprises the ordinary tactile nerves, making up the greater part of the spinal dorsal roots, but represented in certain ones only of the cranial nerves. They are

[1] Studies from the Neurological Laboratory of Denison University, No. XVII.

free nerve endings in the skin without specialized sense organs and may be regarded as in all probability the most primitive type of sensory ending.

(2) Neuromasts. This system of sense organs includes the lateral canal organs, pit organs, ampullae and all other specialized organs associated with the lateral line canals and innervated by lateralis nerves, together with the sense organs of the internal ear of like phylogenetic origin and innervation. These organs clearly belong to a single system and the evidence thus far accummulated favors the inference that the system as a whole has been derived phylogenetically from the general cutaneous system of nerves. This is not the place to give the detailed proof of this, but the trend of the current argument may be summarized as follows under two heads:

(a) the sense organs themselves are characterized in their adult and highly functional condition by the presence of hair cells differentiated from indifferent supporting cells and extending only part way through the epithelium of the sense organ. These hair cells may not occur in the earliest embryological stages of development of the organs, nor in states of functional and structural degradation. The former point accounts for the statements of several authors to the effect that the lateral line organs pass through a developmental stage which is similar to the adult structure of the terminal buds, and the latter point for the confusion which has arisen in the minds of many authors, giving rise to the belief that there is no clearly marked structural difference between neuromasts of the lateral line series and the terminal buds. Nevertheless, the distinction drawn by SCHULZE and MERKEL between the neuromasts and terminal buds, the former possessing the hair cells and the latter not, stands as an essential criterion in all cases where the organs are well developed. Now these hair cells resemble somewhat in structure and probably also in mode of function the tactile hairs of certain aquatic invertebrates and in fact are probably phylogetically derived from them. PARKER ('03) has shown clearly the probable line of differentiation of these structures from tactile organs for the perception of mass move-

ment of the water to organs of equilibration and hearing. We therefore have structural and physiological evidence that the sense organs of the acustico-lateralis system have been derived from tactile organs.

(b) Now turning to the central connections of the acustico-lateralis nerves within the brain, we have a quite independent line of evidence. It has long been known that these nerves all end in the tuberculum acusticum and associated centers, and it has recently been shown, particularly by JOHNSTON in an important series of papers, that these centers are all derivatives of the general cutaneous or tactile centers of the brain. While my own studies on the teleosts have shown that in these higher fishes the specialization of the acustico-lateralis centers has progressed so far as to obscure the primary relations, JOHNSTON'S observations on the lower fishes leave no room for doubt that the history is as stated above.

From the concurrent history of both central and peripheral relations we are therefore justified in assuming that the neuromasts and their associated nervous apparatus have been derived from the general cutaneous or tactile system of nerves.

(3) The terminal buds (end-buds, beaker organs, etc.) are by no means on so secure a morphological foundation. It is, however, now definitely known that they resemble in every essential respect the taste buds within the mouth cavity. The specific sensory cells are not hair cells, but, like the indifferent supporting cells, they run through the entire thickness of the sensory epithelium from external to internal limiting membrane. They may terminate distally in a short stiff bristle, but never in the tuft of long hairs characteristic of hair cells. The organs usually rest on a raised papilla of dermis, and finally in every case where the innervation is accurately known they are supplied by communis nerves, which have nothing in common either centrally or peripherally with the general cutaneous or acustico-lateralis systems of nerves. On the other hand, these nerves always terminate within the brain in a single center (bilobed in some fishes), the vagal lobe (plus facial lobe in silur-

oids and cyprinoids), which also receives the typical gustatory fibers from the taste buds of the mouth.

If now it can be shown that the terminal buds differ functionally, as well as in this thorough-going structural fashion, from all other cutaneous sense organs, then it would appear that their rank as a separate system of sense organs should remain unchallenged. And such in fact is the attitude of most of the recent students of this question, even without a rigid demonstration of the functional relations. I am, however, at this time in a position to contribute positive facts regarding the functions of the terminal buds, and since one recent author of note has within the year made a very forcible plea for a return to the older standpoint of LEYDIG and others that terminal buds and neuromasts are genetically related, I am moved to review the whole question again.

But first we must examine more thoroughly the central nervous connections of the terminal buds, since the morphological argument really hinges upon this point. I repeat, that the terminal buds of the outer skin of fishes are known to be innervated by a system of nerves which is *entirely distinct* throughout from either the tactile or lateralis nerves. There are no accurate observations which contradict this conclusion, while the positive evidence is quite decisive. The most convincing chapter in the elucidation of this problem is, I think, my own examination of the innervation of the cutaneous organs in Ameiurus (HERRICK, '01), which was undertaken primarily to test this very question. The cyprinoids would give an equally decisive answer to the problem, as I know from personal observation (as yet unpublished), though perhaps here the evidence would not be quite so easy to read.

The nerves from these terminal buds, no matter where they are located on the body, always reach the central nervous system through either the X, IX or VII pairs of cranial nerves, and so far as my personal observation goes, practically all come in by the VII nerve, though all three of these nerves in all types receive gustatory fibers from taste buds within the mouth. Both of these classes of fibers, together with a large number of

unspecialized visceral sensory fibers must be treated together within the brain, since they are so intimately intermingled that analysis has so far proven impossible. Accordingly, they are termed collectively the "communis system" of cranial nerve fibers. Peripherally this system is clearly divisible into two components, (1) the unspecialized visceral sensory which is doubtless much more ancient phylogenetically, and (2) the specialized, which for reasons to appear we may now term the gustatory component. This component may be divided topographically into two divisions, one for taste buds within the mouth, and one for terminal buds in the outer skin. It is the latter division only, of course, with which we are here concerned.

In fishes in which the terminal buds are not exceedingly numerous, as in the cod, their nerve fibers, though they enter the brain by the facial nerve, all turn back in the fasciculus communis to find their terminal nucleus in the vagal lobe, along with all other communis nerves of the body. But in the two groups of teleostean fishes in which these organs are most abundant (viz., the siluroids and cyprinoids) their nerve fibers find their terminal nucleus at the cephalic end of the fasc. communis in a special center, the lobus facialis. In both of these groups all of the terminal buds are innervated from the geniculate ganglion of the facialis root. Of this I am confident in the siluroids (HERRICK, '01). As to the cyprinoids, a rather cursory examination of sections of Carassius convinces me that the same is true, though my study of this type is not by any means exhaustive.

The facial lobe of the siluroids was formerly known as the lobus trigemini, that of the cyprinoids as the lobus impar, in the former case the structure being paired, in the latter unpaired by the fusion in the dorso-median line of the lobes of the two sides. That the facial lobes in these two groups of fishes are really merely differentiated parts of the vagal lobes is manifest, not only from the nature of their peripheral connections as indicated above, but still more evidently from their internal structure and secondary fiber connections. I can speak

with confidence on the latter point, because I have now in an advanced state of preparation a study of their connections and internal organization based on an extensive series of sections by several standard histological methods, including the methods of WEIGERT and GOLGI.

It will not be necessary for me at this time to report these histological observations further than to say that they abundantly confirm the conclusions to which JOHNSTON was led in his studies of Acipenser ('01) and Petromyzon ('02), that the primary and secondary connections of the communis system within the brain are absolutely distinct throughout from those of either the general cutaneous or the acustico-lateralis systems. This I regard as a matter of the highest importance to any estimate of the morphological interpretation of the sense organs innervated from these various centers

We may now turn to the consideration of the function of the terminal buds. This is a matter to which I have devoted considerable attention during the past year and with results which I think may be regarded as decisively answering the question. A preliminary account of these experiments was presented to the American Association for the Advancement of Science at the Pittsburg meeting (Abstract appearing in *Science*, HERRICK, '02) and the final report upon the problem is now in press in the Bulletin of the U. S. Fish Commission at Washington. From that report I excerpt the following summary of results.

The entire cutaneous surface of Ameiurus is known to be supplied with terminal buds, and particularly the barblets. In the gadoid fishes terminal buds are known to be present on the barblet and on the free filiform rays of the pelvic and dorsal fins. Accordingly I chose as the chief subjects of investigation Ameiurus nebulosus, the common 'horned pout,' Microgadus tomcod, the 'tom cod,' and Urophycis tenuis, the 'hake,' together with a number of fishes such as Prionotus and Opsanus in which microscopical examination has shown that terminal buds are absent from the outer skin (MORRILL, '95 and CLAPP, '99).

I may say at once that the fishes known to lack terminal buds and the corresponding cutaneous branches of the communis system of nerves in all cases failed to give any response to any kind of gustatory stimulus applied to the outer skin, in marked contrast to the other types experimented upon.

The methods of experimentation upon the siluroid and gadoid fishes in all cases were exceedingly simple, the attempt being to approach as nearly to the normal feeding habits of the species in question as possible. In particular, care was taken to select only such gustatory stimuli as the fishes were already familiar with and for which there were ready formed well defined reflex paths.

The type of reaction to gustatory stimulation of the terminal buds was found to be practically constant whether the organs stimulated were situated on the dorsal fin (Urophycis), on the ventral fin (Urophycis and Microgadus), on the barblets (Microgadus and Ameiurus) or on the general body surface (Ameiurus). The participation of visual sensations in the reflex act evoked by the stimulus was excluded in certain of the cases by the conditions of the experiment; e. g. in Ameiurus the stimulus could be presented to the terminal buds of the body or a barblet when the head was concealed under leaves or debris on the bottom of the tank. I did not think it necessary to blind any of my fishes because the experiments were sufficiently clear without it, and besides BATESON ('90) has already tried that experiment on certain European gadoid fishes, showing that the reactions now under consideration are not affected by that operation. The participation of the sense of smell was excluded in the case of the tom cod by the destruction of the olfactory organ, with no noticeable resultant modification in the reflexes in question.

The problem is then narrowed down to the differentiation between the senses of taste and touch in my experiments, and this I think can easily be accomplished. My most common mode of procedure was to touch the parts of the body where terminal buds are known to be abundant with sapid substances such as bits of meat, clam, etc., on the end of a long slender

wire, when possible so arranging the experiment that the fish could not see the point of contact. The fish immediately turned with a characteristic movement and snapped up the morsel. But the areas in question, particularly the barblets and free filiform fin rays, are known to be very richly supplied with general cutaneous nerves in addition to the communis nerves for the terminal buds; in other words they have a very rich tactile innervation and doubtless are very sensitive to touch. Was the reaction then essentially tactile or gustatory or both? To test this point I replaced on the end of the wire the customary bit of meat with a wisp of cotton wool or a piece of colorless and tasteless gelatin which had been previously softened up in cold water. The fishes sometimes would take it at the first contact, though they would rarely repeat it and soon ceased to notice the cotton or gelatin at all. If now the cotton were soaked in meat juice and the contact repeated, the fish always instantly reacted exactly as he did to meat in the first instance and no amount of training would suffice to cause him to discontinue the reaction to the cotton when dipped in filtered meat juice.

In brief, the experiments which were hundreds of times repeated in a great variety of forms, show that the fishes normally react to both tactile and gustatory stimuli upon the parts of the body in question; but by training they can be induced to discriminate between the two classes of stimuli, ignoring the simple tactile stimulus, but reacting to this plus the gustatory. I varied the experiment, among other ways, by the use of a fine-pointed pipette, directing a jet of water against the fish and then similarly applying a jet of filtered meat juice. In the former case the jet was ignored or avoided; in the latter it was always eagerly sought, the reaction being similar to that produced by a contact with meat, though more pronounced.

It may be regarded as established that fishes which possess terminal buds in the outer skin taste by means of these organs and habitually find their food by their means, while fishes which lack these organs in the skin have the sense of taste confined to the mouth. The delicacy of the sense of taste in the

skin is directly proportional to the number of terminal buds in the areas in question.

Numerous unrelated types of bony fishes from the siluroids to the gadoids which possess terminal buds have developed specially modified organs to carry the buds and increase their efficiency. These organs may take the form of barblets or of free filiform fin rays. The free rays of the pelvic and dorsal fins of gadoid fishes are thus explained, and indeed this is possibly the motive for the migration into the jugular position of the pelvic fins of the gadoids. In all cases where terminal buds are found on barblets or filiform fin rays gustatory nerves belonging to the communis system are distributed to them.

The fishes in which the cutaneous terminal buds are most highly developed are in general bottom feeders of rather sluggish habit and in some cases they are nocturnal feeders. The high development of this sense is compensated for in some fishes by the reduction of others. The visual power of the fishes is especially apt to suffer degradation. This degradation may be organic, a positive degeneration of the visual apparatus, as in Ameiurus, or it may be merely functional. In the latter case, though the organs of vision are not necessarily modified, these organs are not actually used in procuring food, the fish being unable to effect visual reflexes toward food substances or to correlate visual stimuli with the movements necessary to react toward food substances. The fish may be perfectly able to effect other visual reflexes, such as avoiding enemies, but is apparently unable to understand the significance of food when perceived by the sense of sight only. This particular central reflex path has never been developed, or has atrophied from disuse. Nature has here effected for the species something similar to what is accomplished in individual men occasionally by disease, in the production of certain aphasias.

This study has been directed primarily toward the solution of a simple physiological problem; but in a purely incidental way some points of interest to comparative psychology have come up. We have seen that in the cat fish, hake and tom cod the reflex of seizing the food is normally set off by a com-

bined stimulus of tactile and gustatory end-organs. At first the fish may react similarly to a pure tactile stimulus and the tactile plus the gustatory. After a brief training, however, he acquires the ability to discriminate between the former, which is never followed by satisfaction, and the latter, which is followed by the pleasure of feeding. Clearly the fish learns by experience. We find also some differences between the different species of fishes in this respect, depending on the relative importance of the tactile and gustatory elements of the sensation complex in the normal reflex life of the fish.

It would be interesting to inquire the part played by memory in these reactions. In the case of Ameiurus, where the tactile and gustatory elements of the reflex of seizing food can be experimentally isolated by training, it would doubtless be possible to measure quantitatively the duration of the persistence of this acquired discrimination. I have made no accurate observations on this point, but can say in general that the memory of these fishes seems to be fairly good. (By the term memory I do not mean to prejudice the question of the part played by consciousness here. The original reaction may be largely or wholly an unconscious or automatic response and the "memory" may be an organic memory more closely allied to habit). At the beginning of the tests with cotton the cat fishes generally seized the cotton just as they did the meat. At the close of the first day's experiments they had learned to ignore the cotton as a rule, and half an hour after the close of this series of tests they still would pay small attention to the cotton; but by the day following, if tested first with meat, they would take the cotton for a few times or would react to it slightly during the first few tests, but would learn to let it alone sooner than on the first day. But toward the close of the experiments after several weeks of practice I rarely got any reaction at all with the cotton under any circumstances, even if the fishes had not been tested for several days. With the gadoids the number of experiments was much smaller and they were continued for a shorter time, but I never got so good evidence of memory of the discrimination. On successive days the tests were much

alike. The inability of the tom cod to remember to ignore a tactile contact which is not followed by satisfaction so long as the cat fish remembers a similar discrimination I take to be an indication that the tactile element plays a much larger part in the reflex complex in the gadoids. The known distribution of the terminal buds favors this view also, for while they are very abundant on the barblets and body of the cat fish they are rather sparse on the free fins of the gadoids and the general cutaneous nerve supply on the fins of these fishes is greatly in excess of the communis nerve supply.

I noticed also that all of the fishes that ate freely in captivity soon accustomed themselves to novel methods of feeding and in the case of the cat fishes and the hake especially, as soon as I approached their tanks after the experiments had been in progress some time, the fishes would rise to the top of the tank and eagerly await the expected food. This restlessness became so great with the cat fish that the experiments became increasingly more difficult and there was evidence that vision and possibly smell assumed greater importance after this expectation of food had made its appearance.

From the experiments just summarized we may, I believe, conclude that these fishes taste with the terminal buds essentially as they do with taste buds within the mouth and thus we have added the last link in the chain of evidence necessary to fix the position of these sense organs, the morphological and the physiological evidence giving concurrent testimony to the essential isolation of this system from either of the other types of cutaneous nerves. We are not at present able to assert with confidence the phylogenetic origin of the gustatory system of nerves and sense organs, though the structure of the brain centers seems to favor the belief that the system has been differentiated from the general visceral sensory type of nerves. Of this it cannot be said that we have adequate proof and experience teaches us that, in the absence of evidence, speculations in this field are not very profitable.

As intimated above, the trend of most of the recent work on the nervous system of the fishes accords fairly well with the

conclusions here expressed, with one notable exception. Mr. E. P. ALLIS ('01) has recently published an important paper on certain features of the sense organs (particularly the ampullae of LORENZINI) and cranial nerves of Mustelus, which takes its departure from our present problem, as indicated from the following quotation for the introductory paragraph:

> "I have long had a very decided impression, opposed to that of most workers on the subject, that these ampullary organs must be genetically related to the terminal buds of ganoids and teleosts rather than to the pit organs of those fishes; and I thought that I should easily be able to get some positive evidence of this in the general course and position of the nerves that innervate them in advanced selachian embryos. This positive evidence I have wholly failed to get, for the very simple reason that, in the main nerve trunks, I could not distinguish in my sections the ampullary fibers from the lateral canal ones. Disappointed in this at the very beginning of my investigation, I nevertheless decided to quite carefully trace the lateral canals and the nerves that innervate them and the ampullae, as far back as my sections went, that is, nearly to the level of the first gill slit. Careful consideration of these observations has fully convinced me, though indirectly, that the ampullary organs do represent the terminal buds of ganoids and teleosts, and not the pit organs."

These conclusions have been criticised at some length by JOHNSTON ('02) and by myself (this Journal, vol. XII, p. iii) but ALLIS ('03) now returns to his original proposition fortified by fresh facts from the study of the lateral line system of Polyodon, though the evidence is still all indirect. Fortunately, at this time we are able to meet speculation with fact, and, as we have seen above, to put the morphology of the terminal buds on a secure foundation.

ALLIS' argument rests ultimately on two main supports, viz.: (1) the supposed homology of the cerebral center from which the ampullary organs of selachians are innervated with that from which the teleostean terminal buds are supplied; and (2) the supposed similarity of the ampullae themselves and the terminal buds.

(1) On the first point Mr. ALLIS is able to oppose to the observations of all students of selachian nerves that the ampullae are supplied from lateralis branches only the conjecture that the twigs for the ampullary organs terminate in the brain

in a special center, the so-called lobus trigemini, and that this center is homologous with the structure of that name in Acipenser and teleosts.

Now it proves that neither of these assumptions is true, or at best they are only partially true. The "lobus trigemini" of elasmobranchs is homologous with the part so named in Acipenser, but in both cases the part is a derivative of the tuberculum acusticum and is related to the peripheral nerves from lateral line organs. The work of JOHNSTON leaves no room for doubt on this point, and we may adopt his designation for this lobe, "lobus lineae lateralis." The so-called lobus trigemini of certain teleosts (cyprinoids and siluroids) is now known to be a totally different structure (KINGSBURY, '97; HERRICK, '01), a center for terminal buds, having nothing to do with any part of the acustico-lateralis system. It is termed by recent writers the lobus facialis, and, in view of ALLIS' perpetuation of the old confusion growing out of a false nomenclature, we may well adopt the suggestion of HOUSER ('01), "The term *trigeminal lobe* has been so variously used that it should be dropped from our nomenclature."

We are fortunately no longer shut up to speculation regarding the exact relations of these nerve roots in selachians. In the course of a report upon his analysis of the cranial nerves of Squalus acanthias, STRONG ('03) writes, "The ramus mandibularis externus VII is apparently derived practically entirely from the more dorsal of the two lateral line roots [of the facialis], the ramus buccalis receiving the major part of the remainder of this root, while the ramus ophthalmicus superficialis VII is principally composed of the bulk of the more ventral lateral line root. This would apparently negative the view that the ampullary organs are modified end-buds and the dorsal root an end-bud root." This destroys completely the foundations of ALLIS' labored argument from the structure of the r. ophthalmicus superficialis. In brief, we may conclude from the works of HOUSER, JOHNSTON, STRONG and others, that the terminal bud and lateralis centers in the brains of cyclostomes, selachians and ganoids are as distinct as I find them to be in the teleosts and

that the ampullae of selachians are related to the lateralis and not to the terminal bud centers.

(2) The supposed similarity of ampullary organs and terminal buds we have already touched upon. The fact is that these organs do not resemble each other in their well developed adult forms in any known case. In embryonic or reduced conditions the neuromasts may resemble terminal buds on account of the absence or reduction of their hair cells. But even in these cases the innervation in all instances where it is accurately known removes the ambiguity perfectly. I repudiate most emphatically the statement attributed to me by Mr. ALLIS ('03, p. 662) that in any fishes nerve hillocks (neuromasts) may be innervated by communis fibers. The exact opposite I regard as one of the most important and distinctive of the results which I have reached in my studies upon the nerve components of fishes.

ALLIS further argues for the similarity of the two systems of sense organs on the ground of the resemblance in the mode of the distribution of ampullary organs in very young elasmobranchs to that of terminal buds in adult ganoids (Amia) and teleosts. This resemblance in distribution pattern undoubtedly exists, and ALLIS' demonstration of the origin of ampullary organs in the ontogeny of Mustelus diffusely scattered over the cutaneous surface in the positions of the mouths of their pores in the adult is a point of no small interest and importance. His description of pit lines in Mustelus in relations similar to the pit lines of ganoids and teleosts is also of importance, showing, as I fully agree, that the ampullary organs cannot be homologized with these pit lines.

But it by no means follows because the ampullae are not homologous with the pit lines that they are therefore homologous with the terminal buds. In fact, my studies of Ameiurus have shown that in this type, in addition to lateral line canals and pit lines of strictly typical arrangement, there are two independent systems of diffusely scattered cutaneous sense organs, which I have termed the small pit organs and terminal buds and which are innervated by lateralis and communis nerves re-

spectively. If we must seek for equivalents of selachian ampullary organs, they may be found in these small pit organs, for the two sets of organs agree in all essential points of structure and innervation, save that in the adult the teleostean organs do not sink down into deep tubes and become massed at their inner ends into dense clusters, but retain more nearly the embryonic condition of the selachian organs. A careful review of all of the known facts will show that the two types of sense organs (terminal buds and lateral line organs of various types) may appear or vanish quite independently of each other.

In ALLIS' last paper ('02, p. 663) he rebuts JOHNSTON'S criticisms in the following language. I have numbered the items in the passage quoted for ease of reference.

"(1) That end-buds are all innervated by fibers that 'find their central endings in the lobus vagi;' (2) that all other forms of cutaneous sense organs are innervated by fibers that 'have their central ending in the nucleus funiculi, tuberculum acusticum, or the cerebellum;' (3) that the respective centers for the lateral line and end-bud fibers are so separate and stable 'that it is utterly impossible for fibers or centers to "undergo modification" of any sort such as I understand ALLIS to mean;' (4) that 'It is impossible that these organs [end-buds and lateral line or pit organs] should ever resemble one another in any other than a superficial way;' (5) and that end-buds are organs 'with visceral function (e.g. taste),' while all other sense organs are organs 'with a somatic function (e.g. touch, &c.)', are certainly nothing more nor less than deductions from the theory he seeks to establish in his several works instead of established facts on which to base that theory."

Now, nothing could be further from my desire than to enter into this controversy in a spirit of captious criticism, yet I think it can clearly be shown that there is a solid foundation in fact for nearly every one of the contentions taken by JOHNSTON in the passage quoted. And it should be clearly born in mind that many of the most decisive facts to which I refer have been brought to light since Mr. ALLIS first formulated his theory of the genetic relationship between ampullary organs and terminal buds.

Now taking up the above points in serial order: (1) We have accurate observations on this point in Acipenser (JOHNSTON, '01), Petromyzon (JOHNSTON, '02), Gadus (HERRICK, '00) and Ameiurus (HERRICK, '01, the lobus facialis be-



ing a derivative of the lobus vagi) and I also have unpublished observations on Anguilla, Carassius and other fishes in sufficient numbers to make it plain that it is true generally that in all teleosts possessing terminal buds these organs are innervated from the lobus vagi or its derivative, the lobus facialis. And there are no precise observations on the other side.

(2) The second point I think is abundantly established by the works of all recent students of nerve components, particularly those of STRONG, JOHNSTON and HERRICK.

(3) The third point is stated perhaps rather more strongly than the facts at command permit; nevertheless, I think it must be admitted that the metamorphosis of organs of touch, particularly tactile hairs, into end organs for the perception of mass movements of water (lateral line organs; cf. PARKER, '03), for the maintenance of bodily equilibrium (semi-circular canals) and for hearing presents far less of difficulty than the transformation of any of the organs of this series into gustatory organs. For the organs of the first series are all stimulated by impacts of a common type, differing only in mode of application, rythmic character, etc., while the gustatory organ belongs to a totally different modality.

(4) The fourth point we have touched upon above. Whatever may be conceived abstractly as "possible," it is clear that in point of fact these two types of organs do not resemble each other either in structure, innervation or central connections.

(5) Finally that the terminal buds are organs of taste is no longer a matter of conjecture, but a fact of proof.

We may, then, summarize our examination as follows: The morphological rank and functional significance of the terminal bud system of sense organs is definitely fixed. They are in no way related to any organs of the lateral line system (pit organs, nerve hillocks, ampullary organs, etc.) but on the other hand they are most intimately related to the taste buds within the mouth. This relationship is shown by their identity in structure, innervation, central connections and functions. On the other hand, the phylogeny of the terminal buds is by no means on so secure a foundation as that of the sense organs of

the acustico-lateralis system and much remains here for future research to clear up. We can however advance with confidence at least this negative conclusion, that the terminal buds have not been derived from ampullary organs or any other members of the acustico-lateralis system.

Denison University,
May 7, 1903.

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ON THE NATURE OF THE PERICELLULAR NETWORK OF NERVE CELLS.

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With Plate III.

In 1895 Held announced that the nerve cells in the central system are densely surrounded by the terminals of the axones which divide into fine branches and form by a local union a complicated network. He also described the club-shaped enlargement of the axone terminals which may be seen in the embryonic nervous system. These terminals, or "Axencylinderendfläche," are characterized by the presence of the minute granules or neurosomes which stain red by erythrosin.

The terminal network or "Pericellular network," or "Golgi-netz of Bethe" is very well shown by Bethe's molybdenum technique, as well as by Golgi's modified silver technique. The appearances produced by the foregoing methods are somewhat different from those obtained by the method of Held. This difference in appearance may be due to the fact that both Golgi's and Bethe's technique cover over the finer and more complicated structures by the precipitation of silver chromate or the molybdenum compound respectively, and thus bring out strongly marked and rather angular meshes of the network. The nature of these networks obtained by Held, Golgi and Bethe will be described later on.

I have also noticed and described this pericellular network which not only surrounds the Purkinje cells and the cells in the corpus trapezoideum, but also the cells in the Ammon's horn and those in the ventral cornua of the spinal cord ('03).

Held's idea that the finer network which surrounds the

cell-body and forms the pericellular network, is composed of the terminals of the axones, and that the granules which stain red are neuroplasm, has been criticized by APÁTHY. APÁTHY thinks the Axencylinderendfläche to be nothing more than the neuroglia fibers which very frequently surround the cell-body as well as the dendrites, and thus denies the nervous nature of HELD's pericellular network.

He says: "In Betreff der von HELD beschriebenen pericellulären Ausbreitungen des Axencylinder und in Betreff der Neurosomen desselben Autors, kann ich indessen versichern, dass erstere nichts mit dem Axencylinder, letztere nichts spezielleres mit dem Nervösen überhaupt zu thun haben. Jene Ausbreitung sind ein Gliagitter (die Neuroglia im ursprünglichen weiteren Sinne verstanden), welches von dem Axencylinder, den es während seines Weges im Centralnervensystem, ausserhalb der Myelin Scheide, umhüllt, auf den Zellkörper der Ganglienzelle übergeht und sich auf die sonstigen Ausläufer der Ganglienzelle, auf die Dendriten, fortsetzt. Ein ähnliches, die Ganglienzellen eng umschliessendes Gliageflecht habe ich auch bei Hirudineen beschrieben und es als die Gliazone der Ganglienzellen bezeichnet, welche auch in das innere der Ganglienzelle Fortsätze senden kann, aber nicht eigentlich zur Ganglienzellen gehört und nicht mit dem Neurofibrillengitter zu verwechseln ist. Durch dieselbe Gliazone der Wirbeltierganglienzelle ist, wie ich glaube, auch die von GOLGI durch Chromsilber dargestellte und urlängst beschriebene Gitterhülle bedingt."

This criticism of APÁTHY is, no doubt, one objection to HELD's hypothesis, since, as has been pointed by APÁTHY, the cell-bodies are intimately surrounded by the neuroglia fibers. Furthermore, HELD's technique is not suited to distinguish the neuroglia fibers from that of the pericellular network, although he claims that these two structures stain differently.

Recently HELD published an elaborate article ('03) in which he not only criticised the results obtained by various investigators, but also confirms fully his own earlier observations. He employed several different methods for both staining and fixing, especially GOLGI's modified silver method and BETHE's tech-

nique were used. The paper is accompanied by a large number of drawings made from his own preparations. In some cases, he noticed a direct continuation of the pericellular network by way of terminals with the medullated nerve fibers. Thus he proves conclusively that one set of structures forming the pericellular network is composed of the terminals of the axones, and, in other words, this particular network is nervous in nature. BETHE ('00) also showed a direct continuation of his "primitive neurofibrils" into the Golginetz. BETHE here used his own molybdenum technique. It is therefore evident that the weight of opinion is in favor of the nervous nature of the network and against the view of APÁTHY.

Another objection to the view of HELD has been raised by BETHE ('00). Although he agrees with HELD in considering the pericellular network to be composed of the terminals of the axones represented by the primitive neurofibrils, yet he does not accept the delicate meshwork structure formed by the union of the side branches of the axone terminals as well as the presence of the neurosomes. HELD's answer to this criticism is not a satisfactory one and demands further evidence. My own results obtained from the studies on the preparations stained with a new technique, reveal several facts which support very strongly HELD's idea as well as my own observations previously published ('03), and are opposed to the views of APÁTHY and BETHE.

The staining reagents used for the present investigation were prepared by the following way:

Minced sheep's brains were boiled in 10% formalin for several days on the water-bath. The solution was filtered off while hot. A concentrated aqueous solution of ammonium molybdenum in excess was added together with a few drops of HCl and the solution boiled again. The solution is at first yellow and then turns to a blue color. After continued boiling (at least 24 hours) an intense blue color is produced. The nature of the substance which gives the blue color has not yet been determined. The preparation is stained with the blue solution thus obtained, in the following way: The materials are

fixed with 10% formalin and the sections are made by either paraffin or celloidin technique according to the usual procedure. The sections are first treated for several minutes with dilute hydrochloric acid, and then transferred to the blue solution where they remain for 24 hours. If the section is over-stained, it may be decolorized with 1% potassium permanganate for a second, and the further oxidation is stopped by transferring the section into dilute hydrobromic acid. The preparation thus stained brings out the structures described below.

Unless otherwise mentioned, the following description is based on the observations of cells from the spinal cord of the dog. A careful study of these preparations shows that the nerve-cell-body, as well as dendrites, are stained intense blue, while the axone appears stained a light blue. The neurokeratin in the medullary sheaths, as well as neuroglia fibers stain bluish black; the former being more intensely stained. The blood vessels and nuclei of their walls, as well as the neuroglia nuclei stain faintly blue, and may easily be distinguished from the others. The terminals of the axones stain more faintly than the axones near their origin from the cell-body, although some of the contents of the nerve terminals or neurosomes stain an intense blue. Thus my technique brings out the several structures at once in different tones, and enables us to analyze the material forming the grey matter.

As Fig. 1 shows, there are a large number of the medullated nerves which were cut in different planes. In all cases we can distinguish these fibers from their surroundings by utilizing the fact that the outer layer of the medullated sheath contains well marked neurokeratin which stains an intense black. A large number of the dendritic branches are also found intermingled with the medullated nerve fibers just mentioned. These dendritic branches are also cut in various planes and are distinguished from the axones by the fact that they are destitute of the medullated sheaths and at the same time they are densely surrounded by the neurosomes. If we examine the cross-section of a dendrite, a large number of the granules which surround its circumference are easily observed. Another

structural element to be mentioned here, is the neuroglia fiber. These fibers are easily found with my stain, since it stains them an intense black, and also on account of their filamentous character. They are distributed thickly around the nerve fibers, dendritic branches, blood vessels, etc., but their well-marked characteristics enable them to be readily recognized.

Besides these structures just mentioned, together with blood vessels and neuroglia nuclei, there are left in the grey substance very important structures, the axone terminals or fine filaments which carry the neurosomes. These terminal filaments are extremely difficult to isolate from the surrounding tissue, since they stain very faintly. To meet this difficulty, it is necessary to examine first the neighborhood of the cell-bodies where, as a rule, a lymph space is formed surrounding the latter, and where also the axone endings alone occur. As we shall see from Fig. 1, a large multipolar cell is surrounded by the clear space where a large number of the terminals (Fig. 1, *d*) carrying the neurosomes are seen. A single bundle of the axone terminals in this drawing comprises a number of fine filaments which unite and run together. From this locality, if we trace the terminals toward the grey substance, the faintly stained bluish filaments containing neurosomes are distinguished. These are the terminals which we are trying to demonstrate.

I have pointed out already in my previous paper ('03), that the motor cells in the spinal cord are densely surrounded by the terminals of the axones which form the so-called pericellular network. The network just mentioned is well shown in Fig. 3. These terminals, as Figs. 1 and 3 show, come in contact with the cell-body where they form very complicated meshes. These meshes not only cover the whole surface of the cell-body, but also extend continuously along the entire course of the dendrites. As I have said already, in the substantia grisea, the cross and longitudinal sections of the dendrites cut in various planes and having different sizes, are to be observed. Some of the sections are so minute that they can be seen only with the highest powers. Even such spicules of the dendritic branches are surrounded by the meshes of the

axone terminals. This proves that the dendrites are entirely covered by the meshes of that network. The axone as well as medullated fibers are differently characterized, since they are entirely free from the coverings of these terminals. This fact is well shown in Fig. 2. The relation of these meshes to either dendrites or the cell-body is shown by both Figs. 1 and 2. Fig. 3 represents one process of the dendrites of the motor cells of the cat, stained with HEIDENHAIN'S iron-haematoxylin. As we see from these two figures, the filaments form an expanded meshwork containing a large number of neurosomes and come in contact with the cell-surface. These meshes unite again with those of the neighborhood and completely cover the cell-body and dendrites. A part of this meshwork on the cell-surface is shown in Fig. 3, which has been drawn from a motor cell of a cat stained with HEIDENHAIN'S iron-haematoxylin. The axone terminals, in some cases, form a coarse network in the neighborhood of the cell-body (Fig. 1), or in some instances, these meshes are formed after the axone terminals have reached the surface of the cell-body (Fig. 2).

Thus my preparation shows that the pericellular network is composed exclusively of the substance of a nervous nature and there is not the slightest evidence that the glia fibers take part in the formation of the meshes. This confirms the observations previously published. This network which I am treating of coincides with that obtained by HELD ('95) and AUERBACH ('99). The question now arises whether this network will coincide also with that obtained by GOLGI ('98) and BETHE ('00).

By means of an elaborate technique, BETHE was able to show a peculiar reticular structure covering the cell-bodies as well as dendrites. To this reticular structure, just mentioned, BETHE ('00), gave the name "Golginetz" According to him, the "Golginetz" is homologous with structures described by MEYER, HELD and AUERBACH. He says: (1) "Alle Ganglienzellen und ihre Protoplasma Fortsätze (auch in den feinsten Verzweigungen) sind umgeben von specifischen Netzen, welche ich "Golginetze" nenne. Eine Ausnahme bilden hierin die Spinal-

ganglienzellen, die Zellen der aufsteigenden Trigeminuswurzel und des Lobus electricus des Zitterrochens, bei denen bisher derartige Netze nicht nachgewiesen werden konnten. Auf die Axencylinder (Neuriten) geht das Golginetz nicht über. (2) Die Golginetze sich berührender Neurone sind meist einander durch Netzmaschen verbunden. (3) Bisweilen kann man Axencylinderzweige direkt in die Golginetze übergehen sehen."

Thus BETHE was able to see a direct continuation of the axis-cylinder to the Golginetz. HELD was also able to see such a direct continuation of the two structures just mentioned. BETHE, however, believes that the Golginetz is composed of the combined bundles of the "Primitive Neurofibrils" which form the meshwork by interweaving with one another. He strongly opposes the view of HELD who regards the meshwork as composed of fine branched filaments which carry the neurosomes. BETHE further denies the existence of the neurosomes which, according to him, are produced by the action of the reagents employed. HELD answers BETHE'S assertion in his most recent article ('00). There HELD says that there are two structures in the pericellular network; one is composed of an entirely non-nervous substance or neurokeratin, while the second is the one which is composed of the nervous substance or axone terminals. The neurosomes are contained within the second nervous network only. He further says that BETHE'S Golginetz coincides very probably with the non-nervous network. As a consequence of the technique which he employed, BETHE was unable to see neurosome granules as well as the fine meshwork. According to HELD the non-nervous network is derived from the neurokeratin or "Gliaschnürringe" which appear surrounding the medullated sheath at certain intervals. HELD illustrates the direct continuation of the Gliaschnürringe with the neurokeratin meshwork. Concerning the second criticism offered by BETHE, that is, the statement that the neurosomes might have been formed as artifacts through the action of the chemicals employed he says that there is no reason to think that the neurosomes are an artificial product, since all the general histological methods for nerve cells bring out this structure

in the same size, form, appearance, and distribution. I also have given some evidence in an earlier paper, that the neurosomes can hardly be regarded as an artificial product, and so far as modern histological technique is concerned, there is no reason to favor BETHE's view on this point.

However, I cannot agree with HELD who thinks that there are two kinds of network, one nervous and the other non-nervous, and that the former may coincide with BETHE's Golginetz. HELD's non-nervous network has been demonstrated by using the molybdenum technique of BETHE. According to HELD, this technique brings out so-called "Gliaschnürringe" which send filaments to form the non-nervous network. This point seems to me quite doubtful, for if the Gliaschnürringe as well as the non-nervous or neurokeratin network were stained, one would expect to find neurokeratin structures along the medullary sheath. The latter, however, were not observed by him. My own technique, which is able to stain both neurokeratin and glia, fails to show the existence of the non-nervous or neurokeratin network about the cell-body. One can see frequently the neuroglia fibers which surround the cell-body; these, however, merely pass over the cell-surface and never stop on it. I noticed very often the neurokeratin rings or "Gliaschnürringe" of the medullary sheath in my preparations but was unable to observe any process from these rings such as has been described by HELD. Therefore I am unable to confirm HELD on this last point.

From the above I believe that there is only one kind of pericellular network which is formed by the terminals of the axones, and further, I believe that GOLGI'S or BETHE'S network is identical with the network described by HELD as the nervous network from the (1) coincidence or indentical distribution, and (2) from the reticular structure observed in all cases. A different appearance shown by different technique, may be due to the fact that the GOLGI and BETHE methods produce a precipitation of silver chromate and molybdenum salts respectively, which covers the finer meshwork, thus obscuring the internal structure and giving it a coarse appearance.

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ILLUSTRATIONS ON PLATE III.

Fig. 1.—Ventral horn cell of a dog.
Fig. 2.—Ventral horn cell of cat. Iron-haematoxylin.
Fig. 3.—Dendritic branch of ventral horn cell of cat. Iron-haematoxylin.

a = neuroglia.
b = blood-vessel.
c = medullated nerve fiber.
d = axone terminals.
e = neuroglia nuclei.
f = cell body.
g = dendrites.

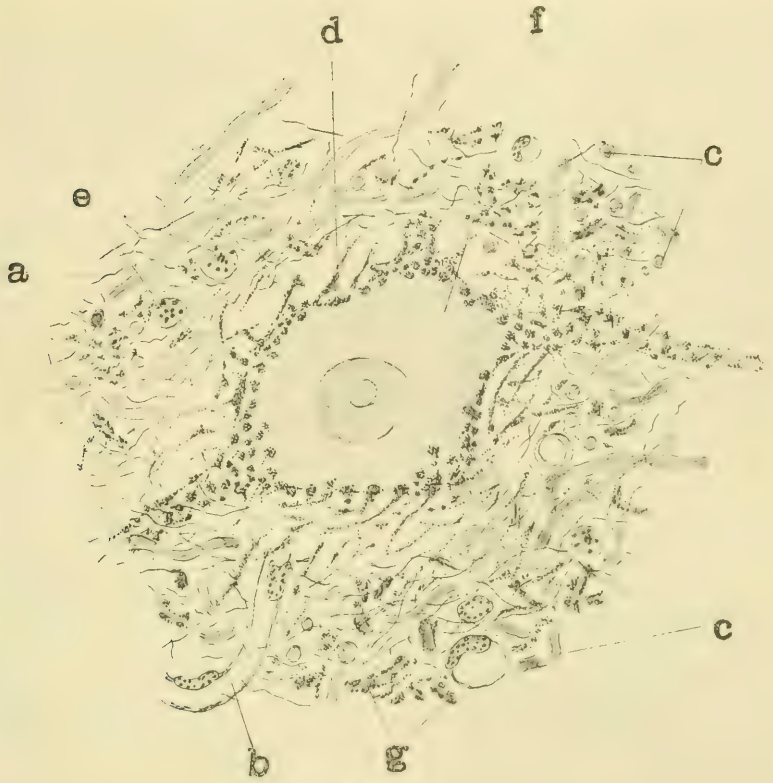


Fig. 1

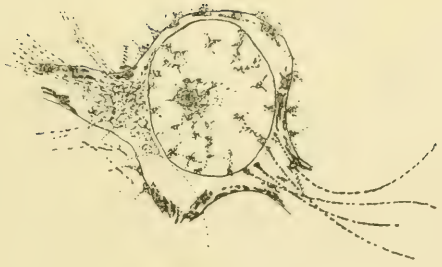


Fig. 2



Fig. 3

THE NEUROKERATIN IN THE MEDULLARY SHEATHS OF THE PERIPHERAL NERVES OF MAMMALS.

By Shinkishi Hatai.

(*From the Neurological Laboratory of the University of Chicago.*)

With Plate IV.

At as early a date as 1876, Ewald and Kühne announced that the nervous system contains a horn-like substance which has a great resistance to chemical reagents and especially to gastric and tryptic digestive fluids. On account of its similarity to the horny material found in other tissues, they termed the substance obtained from the nervous system "Neurokeratin." Josephine Chevalier, in 1884, demonstrated the presence of the neurokeratin in the medullary sheath of the peripheral nerve fibers, by means of chemical analysis. Later (1890) Chittenden again took up the problem of the neurokeratin with Professor Kühne, the first investigator of it, and not only confirmed the previous statement of Ewald and Kühne, but at the same time cleared up many obscure points. In addition to the chemical determination of it, they showed also that the neurokeratin network in the medullary sheath may be demonstrated under the microscope by treating the fiber with boiling alcohol, ether and digestive fluids. By examining under the microscope the slides thus prepared Kühne and Chittenden arrived at the conclusion that there are two layers of the neurokeratin network in the medullary sheath; one closely surrounding the axis cylinder, the other lying immediately beneath the primitive sheath.

Through the investigation of these writers just mentioned, the new field of the study was opened for the neurologist. There are a large number of articles concerning the neuroker-

atin, but it is not necessary to review them in detail. Generally speaking, two different opinions are held by the recent investigators; one, according to which the neurokeratin is not a peculiar substance, but an artefact produced by the reagents employed, an albuminous substance (RANVIER) or a nucleoproteid (WYNN). This view is held by several histologists, for instance, ENGELMANN, GERLACH, KÖLLIKER and LAVDOWSKY. The second view, that the neurokeratin is a peculiar substance in the nervous system and preexists as such, is held by most of the physiological chemists as well as by a number of histologists; for instance, LEYDIG, PALUDINO, JOSEPH, SCHIEFFERDECKER, KAPLAN and others.

In recent years the use of WEIGERT'S and HEIDENHAIN'S haematoxylin has given many opportunities to study the structure of the neurokeratin, and as a consequence, a large number of reports have already been made. Most of the recent investigators are inclined to believe in the preexistence of the neurokeratin in the medullary sheath, on both chemical and histological grounds, and moreover the complexity of the neurokeratin increases as the technique improves.

Before discussing the literature further, I shall give an account of my own results.

For this investigation, the nerve fibers were preserved in 10% formalin and cut into sections 10μ thick after the usual paraffine technique. The sections were stained with the "blue solution"[1] and decolorized sufficiently with diluted NH_4OH. In some cases the blue solution was used without subsequent decolorization.

The preparations thus treated show the double layers of the neurokeratin network in the medullary sheath, one layer closely surrounding the axis cylinder, while the other lies just beneath the primitive sheath as was stated by EWALD and KÜHNE and others. Such an arrangement of the neurokeratin

[1] Preparation of the "blue solution" and its application to the microscopical sections is given in my other paper,—"On the Nature of the Pericellular Network." *Journ. Comp. Neurol.*, Vol. XIII, No. 2, p. 141.

can best be seen by examining the cross-section of the nerve fibers.

Fig. 1 shows the cross-section of the peripheral nerve of the cat, treated by the method mentioned above. The neurokeratin stains an intense pink, while the rest of the structure remains for the most part unstained; the axis cylinder presents, however, a faint blue tint. It may easily be seen that each fiber shows the double rings of the neurokeratin, one along the outer margin and the other along the inner margin of the medullary sheath. These rings, however, are not complete circles, but appear as broken lines or are composed of dots. The size as well as number of the dots in each ring is variable. In some cases, instead of minute dots, a continuous long line is noticed, and in still other cases filaments more or less tangential to the inner ring are observed. The latter appearance is more common in the rings which immediately surround the axis cylinder. In some cases, these two rings are connected with each other by means of threads of neurokeratin which run perpendicularly to the long axis of the fibers and in cross-sections give an appearance of radiations from the central ring; in other words, wheel-like structures are formed by means of connecting bands between the two rings. The manner of the distribution of the connecting band is so irregular that it is almost impossible to give a general description of all the different appearances. I can merely state that the number of the connecting bands just mentioned is not constant, sometimes six or seven being observed and in some cases more than a dozen. Furthermore, the spaces formed by the connecting bands are also variable in size and shape. Some of the connecting bands are united with others by means of the delicate side-branches which they give off. In some instances, three rings are noticed (Fig. 1,*b*). The reason for this irregular distribution of the neurokeratin in the cross-section of the nerve fibers is easily understood if one examines the longitudinal sections of the same fibers, and to these we now turn.

The longitudinal view of the nerve fibers is shown in Figures 2, 3 and 4. The preparations were made from the peri-

pheral nerves of the dog, using the same technique as was employed for the cross-section of the fibers.

Fig. 2 shows the general arrangement of the nerve fibers, as well as the manner of distribution of the neurokeratin. In this figure, the well known cone-shaped or funnel-shaped structures are shown clearly. The cone, as is known already, is formed by the network of the neurokeratin; the basal or wide end attaches to the outer layer of the neurokeratin sheath, while the narrow tip is attached to the neurokeratin sheath which directly surrounds the axis cylinder. In many cases, instead of the single cone there is the appearance of two cones united by their apices and at their bases attached to the outer margin of the sheath, as is shown in Fig. 2. The shape, size, direction, as well as number in each internode of the nerve fiber, is not constant. In some fibers the distance between the two narrow tips of the cones is quite regular, and the median longitudinal section of such fiber shows it to be divided into equal segments by means of the neurokeratin funnels or cones. (Fig. 2, *f*). Both the outer and inner layers of neurokeratin network are continuous throughout the entire length of the nerve fiber, as they are not interrupted at the nodes of RANVIER (Fig. 2, *a,g.*) The structures of the cones and their relation to the two sheathing layers are shown in Fig. 4. I have mentioned already that double rings of the neurokeratin are noticed in examining the cross-sections of the fibers, and further gave the hint that the dots forming the rings are connected by means of delicate filaments of the same substance, and these connecting filaments are in turn continuous by means of the side-branches. Such a complicated arrangement may be understood by examining the structures drawn in Fig. 2 and Fig. 4. Since the two sheathing layers of the neurokeratin are connected either by radial filaments from the inner sheath toward the outer layer or by the branches which are sent off from the inner surface of the cones toward the inner neurokeratin sheath, there is thus formed a complicated arrangement of the neurokeratin in the cross-sections of the fibers. In most cases, the outermost layer of the neurokeratin has fine meshes, as is

shown in Fig. 2, *b*, while in some cases larger spaces of the network are noticed at the small end of the funnel (Fig. 3) while the basal portion of the funnel has much finer meshes.

WYNN ('00), who studied the medullary sheath by using the PAL-WEIGERT technique, states that each cone is composed of six segments, placed at regular distances apart, and converging from the primitive sheath to the axis cylinder. The present writer has examined a large number of preparations stained with PAL-WEIGERT technique, but fails to confirm this result, although, in some cases, there are six dots placed at regular distances (Fig. 1, *a*) and located in some cases along the inner margin of the primitive sheath and sometimes closely surrounding the axis cylinder. A careful examination, however, reveals that in most cases more than six dots are to be seen, and furthermore, each dot is not a single dot but composed of several irregular lines and minute dots, thus giving a structure such as is to be seen in my preparations. According to WLASSAK'S ('00) investigation, the PAL-WEIGERT technique stains only the substance known as cerebrin, which is a constituent of the myelin, but not of the neurokeratin. If this statement of WLASSAK is true, the PAL-WEIGERT technique shows a distribution of the cerebrin in the medullary sheath, but not the distribution of the neurokeratin. The six rods described by WYNN, therefore, may prove that the cerebrin in the medullary sheath is distributed in a special relation to the cones; in other words, the cerebrin and neurokeratin are closely interdependent in their distribution. WYNN arrived, however, at the conclusion that the substance which forms the cones is neither a fatty body, nor neurokeratin, but a nucleoproteid. The statement given by WYNN, that the six dots given in the medullary sheath brought out by PAL-WEIGERT technique, are not the neurokeratin, seems very probable, for by comparing sections by the PAL-WEIGERT method with mine for neurokeratin, the dots of the former are seen to be of a size comparable with the spaces formed by the neurokeratin net in my slides and thus the two preparations give complementary pictures (Fig. 5). Passing by the contradictory statements of WYNN

and WLASSAK, it is only necessary for me to accept the statements that the cones described by WYNN are not true neurokeratin but a substance (either neucleoproteid or cerebrin) precipitated along the walls of funnels, and as a consequence, to conclude that WYNN is dealing with some substance other than neurokeratin. As a consequence, WYNN failed to obtain the network structure of the neurokeratin. The results obtained by the PAL-WEIGERT technique are, however, extremely interesting, for the preparations stained by this method reveal the manner of distribution of the cerebrin (WLASSAK) which is complementary to that of the neurokeratin and thus indicate indirectly the distribution of the neurokeratin.

The structure of the medullary sheath of the peripheral nerves, as revealed by these sections, seems to be as follows:

The neurokeratin network which contains the myelin consists, first, of two thin layers, one beneath the primitive sheath, the other around the axis cylinder; these two layers are, however, continuous at the nodes of RANVIER; second, of a chain of cones connected with both layers, the base of a cone being attached to the peripheral layer, the apex in the inner layer, each cone being made up of a continuous band of neurokeratin exhibiting meshes of variable size and converging from the primitive sheath to the axis cylinder. The clefts of SCHMIDT-LANTERMANN occur at the situation of the cones, but in some cases they are also visible between the two cones. Furthermore, the cones present a great variability in number, size, and direction. These phenomena, just mentioned, may indicate that the SCHMIDT-LANTERMANN clefts are produced artificially by rupture of the coagulated protoplasm along the walls of the cones. My own observations described above may advantageously be summarized as follows:

(1) The peripheral nerve-sheath contains two layers of the neurokeratin, one beneath the primitive sheath and the other along the axis cylinder. These two layers are connected by bands of neurokeratin which run obliquely from the outer to the inner layer, thus presenting a funnel or a cone-shaped appearance.

(2) The neurokeratin sheath has a large number of pores or meshes and presents a net-like appearance. The size and shape of the meshes are, however, highly variable.

(3) Neither the outer nor inner layers of the neurokeratin are interrupted at the node of RANVIER, but become continuous through it with the corresponding layers of the adjoining internodes.

(4) The present observations do not agree with WYNN's, but confirm the previous statements of EWALD and KÜHNE.

(5) The present technique brings out a more detailed structure of the neurokeratin than has been obtained by other investigators.

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The above bibliography is supplementary to the references given by KÖLLIKER, WYNN and KAPLAN.

EXPLANATION OF THE FIGURES.

PLATE IV.

The following figures are free-hand drawings, using Zeiss Oc. 4 x obj. 1-12.

Fig. 1.—Cross-sections of the ventral root nerves of the cat, showing distribution of neurokeratin.

Fig. 2.—Longitudinal section of the ventral root nerves of the dog, showing form of cones.

Fig. 3.—Largely magnified drawing of a single nerve-fiber taken from the preparation used for Fig. 2, showing the meshwork in the cones.

Fig. 4.—Same as Fig. 3.

Fig. 5.—Enlarged view of a cross-section of a single nerve-fiber taken from the preparation used for Fig. 1, showing neurokeratin framework.

Fig. 6. Cross-section of ventral root nerve of human spinal cord. PAL-WEIGERT. Largely magnified. Showing masses of medullary substance included in neurokeratin framework.

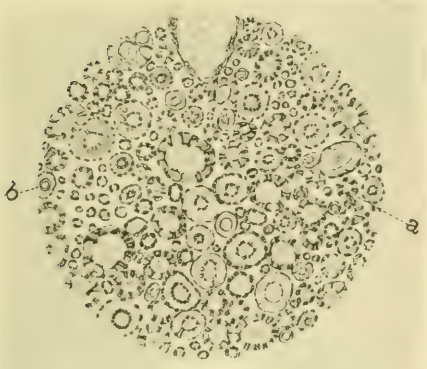


Fig. 1

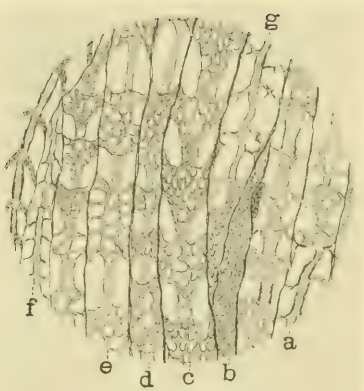


Fig. 2


Fig. 3


Fig. 4


Fig. 5


Fig. 6

LITERARY NOTICES.

Hearing and Allied Senses in Fishes.[1]

The moot question whether fishes possess the sense of hearing has been attacked experimentally by PARKER with the result that he gives a definite affirmative answer for some types of teleosts. This report will impress the reader as a particularly clean piece of experimental research and the conclusions seem to be free from any reasonable question. The experiments were ingeniously planned, carefully controlled and skilfully performed. The general methods of the research, as well as the conclusions, can be gathered from the author's summary of results, which we quote:

1. Normal *Fundulus heteroclitus* reacts to the sound waves from a tuning-fork of 128 vibrations per second by movements of the pectoral fins and by an increase in the respiratory rate. It probably also responds to sound waves by caudal fin movements and by general locomotor movements.

2. Individuals in which the eighth (auditory) nerves have been cut do not respond to sound waves from the tuning-fork.

3. The absence of responses to sound waves in individuals with severed eighth nerves is not due to the shock of the operation or to other secondary causes, but to the loss of the ear as a sense organ.

4. *Fundulus heteroclitus* therefore possesses the sense of hearing.

5. The ears in this species are also organs of prime importance in equilibration.

6. Normal *Fundulus heteroclitus* swims downward from the top of the water and remains near the bottom when the aquarium in which it is contained is given a slight noiseless motion.

7. Individuals in which the nerves to the lateral-line organs have been cut will swim upward or remain at the top while the aquarium is being gently and noiselessly moved.

8. The lateral-line organs in this species are probably stimulated

[1] PARKER, G. H. Hearing and Allied Senses in Fishes. *U. S. Fish Commission Bulletin for 1902, Washington*, 1903, pp. 45-64.

by a slight mass movement of the water against them. They are not stimulated by sound waves such as stimulate the ears.

9. Individuals in which the nerves to the lateral-line organs have been cut swim downward and thus escape from regions of surface wave action. They also orient perfectly in swimming against a current. Since surface waves and current action stimulate fishes in which the nerves to the lateral-line organs and to the ears have been cut, these motions must stimulate the general cutaneous nerves (touch).

10. The vibrations from a bass-viol string when transmitted to water stimulate the ears and the lateral-line organs of *Fundulus*. They also stimulate mackerel and menhaden, but not the smooth dog-fish, which responds only when in contact with solid portions of an aquarium subjected to vibrations.

We have another interesting set of observations in Professor TULLBERG's paper on the Functions of the Labyrinth in Fishes.[1]

The author operated on various teleosts by cutting the semi-circular canals, removing the large otolith and in various other ways and concludes that the labyrinth is not an organ of equilibrium, or of the static sense or for the maintenance of muscular tone or of the spacial sense in the sense of v. CYON. It is probably to some degree an auditory organ (though he gives no satisfactory proof of this). "Originally and primitively, however, the labyrinth of fishes is a sense organ for the perception of movements of the surrounding water, since currents are apparently perceived by the cristae acusticae of the ampullae, but wave movements probably by the maculae acusticae of the utriculus, the sacculus and the lagena. The central organ for this sense organ is apparently the cerebellum."

That the labyrinth is primarily an organ for the perception of currents or streaming movements of the surrounding medium seems on *a priori* grounds highly improbable, since the stimulus is one which may easily act upon the skin, lateral-line organs or other superficial sense organs, but only with difficulty on the deep-seated labyrinth. Moreover the experiments cited seem inconclusive. In the first place, the canals were merely cut and the nerve endings were not destroyed. The same applies to the removal of the otolith. In several of these experiments there were forced movements and disturbances of equilibrium which the author has to explain away. In general too the lesions were symmetrical. More radical operations would seem to be

[1] TYCHO TULLBERG. Das Labyrinth der Fische, Ein Organ zur Empfindung der Wasserbewegungen. *Bihang till K. Svenska Vet.-Akad. Handlingar, Stockholm*, Bd. 28, Afd. IV, No. 15, 1903.

necessary before permitting the conclusion that the labyrinth is not concerned in equilibration and the static sense. In experiment 12, designed to show that orientation with reference to water currents is not done by the lateral-line canals, the n. lateralis vagi was cut behind the shoulder girdle, with the result that the operated fishes still oriented themselves with reference to currents like normal fishes. But it should be noted that in this experiment the canals of the head, of far greater extent and importance, were uninjured.

Professor TULLBERG'S experiments are criticised at some length by Dr. PARKER in connection with a brief report upon his own experiments recently published in the American Naturalist. [1]

A physiological and morphological classification of all of the cutaneous sense organs of fishes as conceived by the present writer is now in press in the current number of the American Naturalist, and the status of such of these organs as belong to the communis or gustatory system is treated more at length in another place in this issue of this Journal. C. J. H.

Taste Fibers and Their Independence of the Trigeminus.[2]

The surgical work and clinical observations upon which this report is based seem to have been more carefully planned and more skilfully wrought out for the solution of the problem of the course of the taste fibers than any of the preceding contributions to this difficult theme. In most of these cases a preliminary test of gustatory sensibility was made before the operation—a most necessary precaution, as the event proved. The patients were whenever possible kept under observation and repeatedly tested for long intervals after the operation. The results in all of the cases furnish a strikingly clear proof of the thesis stated in the title, without the confusion and ambiguity of most previous reports.

In general there is a post-operative transient period of total or partial abolition of taste perception, with a gradual return to the normal gustatory sensibility, but no return of tactile sensibility. He says, "I find it difficult to reconcile my fairly uniform results, that is, uniform in so far as the ultimate preservation of taste is concerned, with the contradictory observations which have been made by so many

[1] PARKER, G. H. The Sense of Hearing in Fishes. *Am. Nat.*, XXXVII, No. 435, March, 1903.

[2] CUSHING, HARVEY. The Taste Fibers and their Independence of the N. Trigeminus. Deductions from Thirteen Cases of Gasserian Ganglion Extirpation. *Johns Hopkins Hospital Bull.*, XIV, No. 144, 145, 1903, pp. 71-78.

others. The only explanation which I can offer is that there may be in a considerable percentage of the cases a temporary diminution in its acuity or a complete abolition of taste as has been intimated above, and that this may have been interpreted under certain circumstances as an evidence of permanent loss of this sense."

The conclusions are: 1. That the perception of taste is unaffected on the posterior portion of the tongue and never permanently or completely lost on its anterior two-thirds after removal of the Gasserian ganglion.

2. That the temporary abolition or lessening of the acuity of taste may be found to exist over the anterior and anaesthetic portion of the tongue for some days after the operation.

3. That this temporary loss of function may possibly be occasioned by some interference with chorda transmission brought about by a mechanical or toxic disturbance due to degeneration of the N. lingualis.

4. That a lesion of the trigeminal nerve may be associated with disturbance of taste over the chorda territory without the necessary inference that the nerve is a path for gustatory impulses.

5. That the N. trigeminus in all probability does not convey taste fibers to the brain either from the anterior or posterior portion of the tongue.

This last conclusion, it will be noted, has been reached almost uniformly of late by researchers in three independent lines of work, the morphologists, the embryologists and the comparative anatomists, and it is a source of satisfaction to see the confusing clinical evidence at last brought into harmony with these in so unambiguous a manner.

C. J. H.

De Fursac's Psychiatry.[1]

Almost every language has had its little compend based on the remarkable changes in psychiatric views, produced by rather a daring but decidedly inspiring reform started by KRAEPELIN. This little book adopts the classification of KRAEPELIN, which is partly etiological, but largely a grouping of the mental diseases according to their outcome. The little book has in some respects an intrinsic value, owing to the attempts at harmonizing current French views with those of the Heidelberg school. The book is dedicated to Professor JOFFROY, and is in a way a semi-official acknowledgement of KRAEPELIN'S attitude.

A. M.

[1] Manuel de Psychiatrie, by Dr. ROGUES DE FURSAC. *Paris, F. Alcan*, 1903.

The Evolution of Man and his Mind.[1]

This bulky volume, which contains much that is admirable, is designed to be a popular exposition of the course of human evolution, particularly from the point of view of certain sociological defects of our present status. This makes a striking background for an exposé and arraignment of certain corrupt tendencies in our political and social organization. The literary style is colloquial and catchy and the book should do good in directing popular attention toward these abuses. As a whole, however, it is so ill-balanced and full of inaccuracies that it can hardly be commended as a helpful scientific contribution.

C. J. H.

The Brain and Nerves of the Anamnia.[2]

Professor JOHNSTON's summary of recent progress in our knowledge of the central and peripheral nervous system of the Ichthyopsida is one of the notable papers of the year. The point of view from which he writes is so distinctively his own that his article is more than a mere abstract or critical review; it is a positive contribution toward the solution of some of the major problems of comparative morphology. This point of view he has already presented in this Journal (March, 1902), under the title, "An Attempt to Define the Primitive Functional Divisions of the Central Nervous System," being essentially the correlation of central with peripheral differentiation of the nervous system. We venture the prediction that the next decade will see this principle worked out successfully in several fields at present open merely to the methods of descriptive anatomy. The conclusions of students of nerve components as formulated at the present moment may or may not stand the test of time, but the essential aims and methods of work which they have introduced into comparative neurology will surely in the end yield results of permanent value. Professor JOHNSTON's *Referat* is therefore very timely. C. J. H.

[1] CLEVENGER, S. V. The Evolution of Man and his Mind. A History and Discussion of the Evolution and Relation of the Mind and Body of Man and Animals. *Chicago*, 1903.

[2] JOHNSTON, J. B. Das Gehirn und die Cranialnerven der Anamnia. *Merkel und Bonnet's Ergebnisse*, Bd. XI, for 1901. *Wiesbaden*, 1902, pp. 973-1112.

The Dorsal Spino-cerebellar Tract.[1]

Sections of the spinal cords of dogs at different thoracic and cervical levels show that the longest fibers of the direct dorso-lateral cerebellar tract, i. e., those arising in the lowest levels of the spinal cord, are most superficial in position and that the shorter fibers are added successively along the inner side of this zone.

The authors verify previous findings of degeneration in the cells of CLARKE'S column below the lesion after section of the dorso-lateral cerebellar tract. In these cases the fibers of the tract between the degenerated cells and the lesion show no degeneration under the MARCHI procedure, WEIGERT stain, anilin blue-black, picrocarmine, etc. To test the condition of these fibers further the authors made a right lateral transection of the Xth thoracic segment 260 days subsequent to a total transection at the IId thoracic level. The animal (dog) was sacrificed 20 days after the establishment of the second lesion. The right cerebellar tract above the second lesion was found fully presenting all the signs of WALLERIAN degeneration under the MARCHI reaction. The left cerebellar tract appeared normal and without any degeneration.

"It would seem therefore that atrophy, severe and long-lasting, probably permanent, of CLARKE'S cell-column induced by spinal transection in the the lower cervical or upper thoracic region, far from destroying the dorsal cerebellar tract, leads to no obvious or easily demonstrable degeneration of at least the main body of the fibers of the tract. Further, after the severe atrophy of CLARKE'S column has set in and become established, transection of the tract in the very region of atrophy of the cell-column still causes full WALLERIAN degeneration of the fibers head-ward of the transection." These results obviously have an important bearing on the theory of the physiology of the neurone and its biological interpretation. C. J. H.

The Optic Chiasma in Symmetrical and Asymmetrical Teleosts.[2]

The author in continuing his observations on the optic chiasma of fishes develops several results which bear directly on the morphology and phylogeny of the flat fishes. He has previously shown[3] that in

[1] SHERRINGTON, C. S. and LASLETT, E. E. Remarks on the Dorsal Spino-cerebellar Tract. *Journ. of Physiol.*, XXIX, 2, March, 1903.

[2] PARKER, G. H. The Optic Chiasma in Teleosts and its Bearing on the Asymmetry of the Heterosomata. *Bull. Mus. Comp. Zool.*, XL, 5, 1903.

[3] The Crossing of the Optic Nerve in Teleosts. *Biol. Bull.*, II, 1901, pp. 335-336.

the symmetrical teleosts the right and left optic nerves are dorsal in an approximately equal number of cases. He now extends the observations to the flat-fishes and finds that the two families into which the sub order Heterosomata is divided by recent systematists differ conspicuously in this character. In the Soleidae the chiasmata are dimorphic, as in symmetrical teleosts; i. e., the right optic nerve is dorsal in about half of the observed cases and ventral in about half. In the Pleuronectidae, on the other hand, the chiasmata are monomorphic for each species; in dextral species the left nerve is dorsal, in sinistral species the right nerve is dorsal. All species of this family that turn in only one direction have their dorsal nerves connected with their migrating eyes. In all species that have both dextral and sinistral individuals, the dorsal nerve is connected with that eye which in the greatest number or in the nearest of kin migrates. The unmetamorphosed young of the Pleuronectidae are not symmetrical in the same sense that symmetrical teleosts are, for they have monomorphic chiasmata. The Soleidae are not degraded Pleuronectidae, but degenerate descendants of primitive flat-fishes, from which the Pleuronectidae have probably been derived. The monomorphic condition of the optic chiasma of the Pleuronectidae can be explained only on the assumption of natural selection. The flat-fishes afford striking examples of discontinuous variation. C. J. H.

Brain Weights of Eminent Men.[1]

Dr. SPITZKA has tabulated 96 cases and made comparisons with the statistics of 800 brains of ordinary persons as given by BISCHOFF and MARCHAND. "The average (arithmetical) brain weight of the 96 individuals is 1473 grams, exceeding the various averages given for the European brain by 75 to 125 grams, and this without allowing for the advanced age of this series; the average of 92 being 63 years." "It is further shown that the period of decrease [in brain weight] with age is deferred for fully a decade among the more intellectual persons, a point already alluded to by DONALDSON, and significant in connection with the longevity of healthy persons endowed with high intelligence." The paper is accompanied by several instructive curves and tables.

C. J. H.

[1] SPITZKA, EDWARD ANTHONY. A Study of the Brain Weights of Men Notable in the Professions, Arts and Sciences. *Philadelphia Medical Journal*, May 2, 1903.

The Lateral Sensory System of the Eels.[1]

In this paper of 48 pages and three good plates we have a detailed description of the lateral line canals and associated sense organs in the conger eel and a more brief account of three related species of Muraenidae, viz., Ophicthys serpens, Myrus vulgaris and Muraena helena. The nerves supplying these sense organs have been traced only in their peripheral portions and we are promised a later research upon the innervation of these structures in the conger.

In connection with the innervation of the pit organs there is one correction of minor importance on page 42 of the reprint, to which attention might be drawn. Mr. ALLIS describes a pit line running parallel with the squamosal lateral canal which is innervated by a nerve formed from an anastomosis between a branch of the facial, which is regarded as a portion of the ramus opercularis facialis, and a branch of the glossopharyngeus or vagus. In discussing the morphology of these pit organs the author says, "If they be pit organs, it is practically certain that they cannot be innervated by the facialis, for there is no single instance that I know of, of lateral sensory fibers accompanying the ramus opercularis of that nerve." As a matter of fact I have described just such a condition in Menidia (this Journal, vol. IX, p. 294, seqq.), HAUSBROT's descriptions strongly suggest the same thing, and I have no doubt that a careful search of the literature would reveal other such cases. Confusion arises in this connection (and this is the occasion of this note) from the fact that there are two opercular rami in teleosts which are not always distinguished. The ramus opercularis profundus VII is a purely motor nerve, and this is the only one of these branches which is mentioned by STANNIUS. On the other hand, the ramus opercularis superficialis VII is a mixed nerve, containing in Menidia both general cutaneous and lateralis fibers and in other cases apparently it may contain communis fibers also or be fused with the motor fibers belonging to the ramus hyoideus VII. This superficial nerve frequently anasomoses with the vagus or glossopharyngeus and in Menidia at any rate it is clear that the vagal fibers are all of general cutaneous nature.

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[1] ALLIS, E. P. The Lateral Sensory System in the Muraenidae. *Intern. Monatsschrift f. Anat. u. Physiol.*, XX, 4-6, 1903.

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THE NEUROFIBRILLAR STUCTURES IN THE GANGLIA OF THE LEECH AND CRAYFISH WITH ESPECIAL REFERENCE TO THE NEURONE THEORY.

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With Plates V and VI.

A previous publication treats in detail of the fibrillar networks in the neuropil of the leech. In the present paper it is purposed to give a more general description of the fibrillar structures found in the nervous system of the leech and crayfish and to point out the relation of these structures to the neurone theory.

The neurone theory, grounded upon the fundamental researches of GUDDEN, GOLGI, and HIS, was first formulated by WALDEYER ('91) in the following words: "Das Nervensystem besteht aus zahlreichen, unter einander anatomisch wie genetisch nicht zusammenhängenden Nerveneinheiten (Neuronen)." As WALDEYER, VERWORN, and NISSL have shown, the all-important point embraced in the neurone theory is not the anatomical independence of the nervous elements, but the assumption that the nervous system is entirely composed of cell individuals. Whether the processes of these cells are only in contact, or by growing together have become continuous, is a secondary matter. Nevertheless, on the threefold evidence of histogenesis, neuropathology, and histology, most neurologists maintain that the nervous system is composed of anatomically independent, cellular units.

1. *Histogenesis.* That the nerve elements develop from single neuroblasts and not from chains of cells was first asserted

by HIS ('89, '90). His work has recently been confirmed by the excellent research of HARRISON (:01). The latter was able to show that in two cases dorsal processes from bipolar neuroblasts of the sensory ganglion broke through the bounding membrane of the nerve chord, while ventral processes from the same cells were traced to the periphery. Both HIS and HARRISON have proved that the axis-cylinders and dendrites of motor elements originate as processes from a single cell; they traced the axis-cylinder processes to the very point where the nerve fibers appear; but in no case did either investigator demonstrate direct connection between these processes and the embryonic nerve fibers. HARRISON states moreover that: "Die ersten motorischen Fasern sind schon vorhanden, ehe überhaupt lose Zellen in der Gegend der Austrittsstelle zu finden sind."

Directly contrary to the observations of HIS and HARRISON, and in agreement with those of BALFOUR ('76) and DOHRN ('91) are the preliminary statements of BETHE (:02) as to the histogenesis of the nerve elements in the chick: (1) Before the axis-cylinder processes of the neuroblasts break through the bounding membrane of the chord, the fundaments of nerve fibers are formed as chains of cells; (2) coincident with the breaking through of the processes, many primitive fibers may be observed in the myotomes; (3) processes of the bipolar cells which form these nerve fibers in the myotomes may be traced into the chord with the same distinctness with which the processes of the neuroblasts (of HIS) may be traced out of it, and often the union of processes from neuroblast and primary nerve cell may be observed; (4) the primitive nerve fibers are differentiated simultaneously from an entensive chain of cells extending from the central organ to the periphery; (5) these cells increase in number only by karyokinesis; not until the 7th to 9th day of development are the neuro-fibrillae formed. BETHE concludes from these observations that each nerve element represents a group or society of cells, rather than a single cell individual. His statements are as yet unsupported by published figures, but they agree both with the observations of

other noted neurologists and with his own recent work on the regeneration of peripheral nerves. It is at least clear that as far as the evidence of histogenesis goes the neurone theory is still open to dispute. It is grounded on certain recognized facts, but these facts relate only to the early stages of development. Neither HIS nor HARRISON says anything as to the origin of the neurofibrillae, structures upon which the opponents of the neurone theory put much weight.

2. *Neuropathology.* GUDDEN ('89) was the first to demonstrate the fact that the cutting of a motor axis-cylinder caused the degeneration not only of the peripheral fiber, thus isolated from its cell, but also of the cell and its dendrites. In new-born animals the entire nerve element atrophied and was resorbed, but never in any case were the pathological changes observed beyond the dendrites of the injured neurone. According to NISSL, FOREL ('86) first coupled these facts with the evidence of GOLGI'S preparations and formulated the idea of the nerve-cell individual, to which WALDEYER later gave the name of neurone. The two facts of neuropathology which have been used as arguments in support of the neurone theory are: (1) that nerve fibers separated from their ganglion cells degenerate and (2) that the phenomena of degeneration never have been observed to pass beyond the processes of the injured elements.

The experiments of GUDDEN show that it is not merely their isolation from their cells which causes nerve fibers to degenerate, for the cells themselves often atrophy in young animals. BETHE ('98) by isolating the neuropil of a nerve center in the brain of the crab found that the nerve elements may remain actively functional for several days, proving that the nerve elements are physiologically independent of their cells. His recent experiments in neuropathology, of which he has given only a preliminary account (: 02), show that peripheral nerves will degenerate some time after isolation from their nerve cells; furthermore, that in the young dog such degenerate nerve fibers will, in the course of 6 to 9 months, *regenerate all the structures of a normal nerve fiber—primitive fibrillae, perifibrillar substance and Schwann's sheath.* Not only are the regenerated fibers normal

in structure, but stimulation of the distal stump of the nerve (Ischiadicus) causes contraction of the muscles which it supplies. Upon dividing the regenerated nerve a second time, degeneration ensued in the distal portion only. By this evidence of BETHE's the phenomena of degeneration, in themselves, are rendered worthless as arguments in support of the neurone theory, while his observation of the regeneration of peripheral nerves is incompatible with the assumption that each nerve fiber develops in its entirety as a process of a single ganglion cell.

That the phenomena of degeneration have not been observed to pass beyond the dendrites of the injured nerve elements is most easily accounted for by assuming the non-existence of continuity between the dendrites of the nervous elements. But, as NISSL argues, the opponents of the neurone theory may, with equal right, assume the presence of connecting fibrillar structures in the central organ, of whose peculiar qualities we as yet know nothing, at least in vertebrates. These structures (the "nervöse Grau" of NISSL) are differentiated cell products, and as they are independent of the ganglion cells, they are immune from the pathological changes which affect the processes of the latter. What are the histological facts in support of these assumptions?

3. *Histology.* We have seen that the neurone theory was based by FOREL and WALDEYER mainly upon the discoveries of HIS, and the silver impregnations of GOLGI and RAMÓN Y CAJAL. It is now known that the methods of GOLGI are extremely unreliable, that the impregnations are rarely complete and often extend to non-nervous structures. When, therefore, APÁTHY ('97) demonstrated by new methods the finer structure of the nervous system, many neurologists maintained that the neurone theory had received its death blow. The value of APÁTHY's work, however, has been in throwing into doubt the evidence of GOLGI preparations, and showing the importance of more certain and refined methods for the study of the nerve elements. APÁTHY proved that the supposed nervous units of GOLGI preparations are themselves composed

of infinitely smaller conducting elements, the primitive fibrillae, which form networks in the cells. He also figured cases of direct communication between the processes of nerve cells in the intestine of *Pontobdella* and instances of fibrillar networks in the neuropil of *Hirudo*.

In addition APÁTHY maintains the existence of large motor, and small sensory, fibrillae; these two types of fibrillae are connected with each other by networks in the ganglion cells and by the diffuse fibrillar network which, according to APÁTHY, forms the neuropil proper.

The existence of the neurofibrillae is now generally admitted. BETHE ('98) confirmed APÁTHY'S observations as to the presence of the fibrillae in both the nerve cells and fibers, but could not distinguish between motor and sensory fibrils in the crab, *Carcinus*. He also asserts that the fibrillar networks in the neuropil are not diffuse. His series of studies on the neurofibrillae in the nervous elements of vertebrates ('98*a*, '99, : 00) leads him to the conclusion that they are invariably present, but that the networks characteristic of invertebrate nerve cells are rarely found. He suggests that the neurofibrillae of the cells may be directly connected with the fibrillar "Golginetze" which surround the cells, and that these in turn may be in communication with the fibrillae of other (sensory) elements. Neither BETHE nor NISSL was able to demonstrate a clear case of such fibrillar connection, and the assumption that the "Golginetze" are composed of neurofibrillae has been severely criticized by RAMÓN Y CAJAL and others. NISSL (: 03) assumes the existence, in the central organ, of "nervous gray" structures, the differentiated products of nerve cells, corresponding perhaps to APÁTHY'S diffuse fibrillar network. The assumption that such nervous elements exist, is based entirely on theoretical grounds. He points out that it has never been proved that the neurofibrillae of the nervous system are integral parts of the nerve cells, but that there are facts which indicate that they are not: (1) the fibrillae are sharply marked off from the rest of the cell in both structure and staining qualities; (2) the axis-cylinders are prolonged far beyond the limits of the cell proto-

plasm; (3) in diseased and degenerate cells certain fibrillar tracts, which pass in and out through the dendrites, may remain intact and cannot be distinguished from normal fibrillae. NISSL's figures are schematic and, as in the text, it is difficult to separate fact from theory. His book, however, is of great value in that it discloses the weak spots in the neurone theory and shows that little or nothing is known of the extra-cellular elements found in the gray substance of the vertebrate nervous system. Between the dendrites of the nerve cells and the point at which the sensory axis cylinders lose their medullary sheaths, there is practically a total blank in our present knowledge of the nervous elements.

NISSL accepts as an established fact APÁTHY'S hypothesis that the nerve elements of invertebrates are connected by a diffuse network in the neuropil. Not so the supporters of the neurone theory, who are, however, divided in opinion. By far the majority of them admit the existence of the neurofibrillae, but deny that there is continuity between the neurones. Prominent among this school are VON LENHOSSÉK ('99), S. MEYER ('99), and VAN GEHUCHTEN (: 00). Other neurologists, like WALDEYER, HOCHE ('99) and VERWORN (: 00), while admitting that fibrillar continuity may exist, hold, and we think rightly, that the question of contact or continuity between the neurones is a side issue. They doubt the existence of fibrillar "Gitterwerke," however, and still maintain that the nervous system is composed entirely of cell units.

Because of this doubt which still exists in the minds of many neurologists, as to certain of APÁTHY'S observations, the writer has made a special study of the fibrillar structures found in the neuropil of *Hirudo*, the results of which are now in press. The present paper furnishes further evidence as to the structure of the neuropil and is supplemented by a more general study of the neurofibrillae in the nerve elements of both *Hirudo* and *Astacus*. The research was begun at the Zoological Laboratory in the University of Freiburg, Baden, and was completed at the Strassburg Physiological Institute.

Material and Methods.

The ventral ganglia of the leech (*Hirudo medicinalis*) and the abdominal ganglia of the crayfish (*Astacus fluviatilis*) formed the material on which most of my study was based. A part of the *Hirudo* material was treated as described in my former paper (PRENTISS, : 03), the method being based on that of BETHE (: 00*a*). Sections 10μ thick, fixed in corrosive sublimate were impregnated with ammonium molybdate solution (1:4000–1:6000), differentiated about one minute in warm water (55°–60° C) and then stained with an aqueous solution of toluidin blue (1:3000). In the ganglion cells a pure fibrillar stain was obtained by fixing ganglia for one hour in ether fumes, staining *in toto* with toluidin blue (1:3000) and fixing the stain in a 1% solution of ammonium molybdate. The material was then dehydrated, embedded in paraffin and sectioned in the usual manner. This method is simple, but uncertain in its results. It is a selective method, like methylen blue, and not all of the fibrillae are demonstrated. Often, however, preparations were obtained which showed the fibrillae with diagrammatic distinctness.

The preparations of *Astacus* material were all stained ***intra vitam*** with methylen blue. The fibrillae were differentiated by leaving the ganglia 2–4 hours in normal salt solution ; the stain was then fixed in ammonium picrate, which differentiates the fibrillae more clearly than molybdate.

The Fibrillae in the Ganglion Cells.

APÁTHY describes two types of cells in the ventral ganglia of *Hirudo*, distinguished from each other by their size and the structure of the neurofibrillae. In the type to which the smaller cells belong, one large fibril enters the cell and forms a close meshwork of rather large fibrillae about the nucleus. This is a motor or cellulifugal fibril according to APÁTHY; its network about the nucleus is connected by radial fibrils with a finer peripheral meshwork formed by smaller cellulipetal or sensory fibrillae. In this manner he assumes that sensory and motor elements are put into direct communication within the

cell itself. The cells of the second type are the largest in the ganglion. Their fibrillae are of nearly equal size and form a diffuse network throughout the plasma of the cell.

The difference in the fibrillar structures contained in these two types of cells was very apparent in my own preparations. A good example of the smaller type (the motor cells of APÁTHY) is illustrated in Figure 14 (Plate VI). The inner network about the nucleus was quite distinct in the preparation; the fibrillae of which it is composed are somewhat larger and therefore easier to trace than those in the periphery of the cell, but preparations in which practically all of the fibrillae within the cells are stained, show no such sharp distinction in the size of the fibrillae as APÁTHY describes. Certain fibrils might appear a little larger than others, but my preparations do not warrant the assertion that the larger fibrillae *always* form the inner network, and the smaller the outer one, as APÁTHY maintains. Such large fibrillae as APÁTHY describes are often found, however, in preparations in which only a portion of the fibrils are stained. It may also be observed that the smaller the number of the fibrillae to be seen in a cell process, the larger those fibrillae usually are. It is well known that APÁTHY's gold chloride method demonstrates the fibrillae more completely in the cells than in their processes, and the large "motor" fibril which APÁTHY figures entering the cell and forming the inner network, is, in every case, it may be noted, *the only fibril in the cell process.* Several large fibrillae are often formed in the cell processes by the cleaving together of the primitive fibrils; if the impregnation of these were incomplete so that only one fibril is visible, conditions would be produced like those figured by APÁTHY. We have such a case evidently in Figure 3 (Plate V). One large fibril (*b*) is seen in the cell process; this, however, divides into four smaller ones on entering the cell. It is obvious that but few of the fibrillae are stained, which renders it especially easy to follow those which are demonstrated. This cell belongs to the smaller type described by APÁTHY, but it may be observed that only one branch (*a*) of the large fibril joins the inner network about the

nucleus; the others take a more peripheral course, a fact which is not in agreement with APÁTHY'S figures. In the same section another cell of the same type was found (Figure 2, Plate V). In this case, however, there are many fibrils of nearly equal size in the cell process, although the networks within the cell are incompletely stained. Neither in vertebrates nor in crustacea do the neurofibrillae of the nerve cells show any marked correlation in size and function.

In the giant cells of the leech there is no inner network about the nucleus; the fibrillae are very numerous in the cell process and divide to form a network of small irregular meshes throughout the greater portion of the cell. A portion of such a cell is shown in Figure 4 (Plate V) and gives some idea of the great number of fibrillae which these giant cells contain.

The fibrillar structures in the ganglion cells of *Astacus* and other decapod crustacea resemble somewhat those of the larger type of cells in *Hirudo*. Such structures have been described by BETHE ('98), and OWSIANNIKOW (: 00). BETHE describes the fibrillae within the ganglion cells of *Carcinus* as of nearly equal size, and forming a network of somewhat large meshes throughout the plasma of the cell. OWSIANNIKOW finds primitive fibrillae of two sizes in the nerve cells of *Astacus;* the smaller of these are found about the nucleus in the form of a network; the larger fibrils occupy the peripheral portion of the cell, and are the continuations of the fibrillae in the cell process.

My preparations of *Astacus* showed no trace of a network of fine fibrillae about the nucleus. The usual condition observed is seen in Figure 15 (Plate VI). The fibrillae appear relatively large and form a few large meshes in the peripheral region of the cell. This figure corresponds to the descriptions of BETHE and resembles the only drawing which OWSIANNIKOW gives of the neurofibrillae in the cells; the figures of the latter do not support the statements he makes in the text.

Fibrillar Structures in the Cell Processes.

BETHE ('98) was the first to observe that in the crab a

nerve element may contain a greater number of neurofibrillae than are found entering its cell, and to show that this was due to the fact that many neurofibrillae may enter a neurone through the collaterals, and pass out either through the peripheral fiber or through other collaterals without entering the cell proper. He regards such conditions as incompatible with the neurone theory, because the fibrils which do not enter the cell can not be integral parts of it, but must be the product of some other cell or cells. The fibrillar structures in the nerve elements of both the leech and the crayfish confirm BETHE'S observations. From methylen blue preparations of the abdominal ganglion of *Astacus*, certain important facts may be observed without the use of a high magnification. As APÁTHY noted in the leech, many of the nerve elements are paired: a large element in the right half of the ganglion has its fellow, similar in size, form and extent, symmetrically placed on the other side. More interesting still is the fact that *both of these paired elements usually take the stain together*, indicating the existence of connection between them. In many of my preparations of the second abdominal ganglion a pair of large motor elements was often demonstrated. One of these from the left side of the ganglion is shown in Figure 10 (Plate VI); its fellow of the right side was its mirrored image even to the number, position and extent of the collaterals. The collaterals always branch to the same points in the neuropil, a fact directly against the assumption that a diffuse fibrillar network exists. For if this were the case, why should the processes of different neurones always pass to the same spot in the neuropil, and why should the nerve elements be arranged in bilateral symmetry? Such an arrangement would be useless if there were a diffuse network of fibrillae in the neuropil, to put the dendrites of all the nerve elements into general communication with one another.

Figure 10 also illustrates a second point, which, as we shall see, bears upon the fibrillar structures in the nerve elements. The nerve fiber reaches its greatest size in the region designated by *a*, *and this is the point at which most of the collaterals*

enter or leave the neurone; both the cell process (*b*) *and the peripheral fiber* (*c*) *are considerably smaller than the region intervening between them.* The greater size of this particular portion of the elements is explained when the fibrillar structures are studied under a higher magnification (Figure 11, Plate VI). It may then be observed that the fibrillae are more numerous at this point than in either the cell process proper, or in the peripheral fiber. Many fibrillae of the large collaterals (*d'*) pass directly to the periphery through the fiber *c'*; others, like fibril *e*, evidently enter the element through one collateral and pass out through another. The same condition was observed in the nerve elements of the leech (Figure 2, Plate V). The figure is from a preparation fixed in ether and stained with toluidin blue. The plane of section was very favorable, showing the whole of the cell process and short portions of the peripheral fiber and of two collaterals in connection with the cell. Here again an enlargement is found at the point where the large collaterals branch off. As only fibrillar structures were stained, each fibril could be traced with perfect distinctness; a large one (*a'*) passes directly from a collateral at *a* into the peripheral fiber *b* and is, therefore, independent of the ganglion cell.

In the large nerve elements of the leech a fibrillar network is often found in that portion of the cell process from which the collaterals branch. Two such cases have been figured (Figures 5 and 7, Plate V). Figure 5 is a type of the more simple connections which exist between the fibrillae in the nerve elements. Three large parallel fibrillae (*a*, *a'*, *a''*) unite at the point *b*; at *c*, a single mesh is formed, from which are given off several smaller fibrils that continue their parallel courses in the process. In this, as in all well differentiated molybdate preparations, the perifibrillar substance is not stained, and the boundaries of the nerve elements are indicated by the course of the fibrillae only.

The processes of the giant ganglion cells of the leech often exhibit extremely complicated fibrillar networks soon after they enter the neuropil (Figure 7, Plate V). In Figure 7 three large fibrillae from the longitudinal commissure unite

with the process; one of these fibrillae (a') joins a small fine-meshed network at c; the fibrillae coming from the cell at a are all put into communication with one another soon after they enter the neuropil by the network at c. Such connecting networks form direct paths for nervous impulses passing from one nerve element to another, and in entire independence of the ganglion cells. These networks have been observed only in the processes of the larger cells. Similar fibrillar structures have been seen by BETHE, whose observations have not as yet been published. The large single fibrillae which unite with the fibrils of the process at right angles often divide forming T-shaped branches. In one case such a fibril was traced into direct connection with the process of another nerve element (PRENTISS, '03, Figure 19).

Figure 1 (Plate V) shows an interesting case of fibrillar continuity within the process of a giant ganglion cell. The process is so sectioned as to show only a portion of its cell, but may be traced into the neuropil together with the three large neurofibrillae which it contains. Immediately within the neuropil, it is joined by two longitudinal fibrillae (a and b), which branch and unite with two of the fibrillae from the cell; a cross fibril, c, puts into direct connection with each other a and b, which are fibrillae from the longitudinal commissures and are evidently in connection with other ganglia, lying anterior and posterior. A nervous impulse, therefore, which was transmitted from the ganglion next anterior to this one, or even from the brain, would be conducted through fibril a, stimulate the nerve element, and pass at once through c and b to the nerve elements in the next posterior ganglion. I have never observed such commissural fibers branching dichotomously like the dendrites of motor elements, but they may constantly be seen in connection with cell processes, as in this case. The fibrillar structures shown in Figure 1 were stained as opaquely as the fibers in GOLGI preparations, and since they were situated in a perfectly clear space, the connections between the various fibrils were, under a magnification of 2000 diameters, as distinct as a diagram. The further continuations of the fibrillae in the cell

process were obscured by longitudinal fibrillae; they cross irregularly, but whether a network was formed could not be determined with certainty.

In the crayfish was found one case of apparent connection between the dendrite of a large motor neurone and a longitudinal connective fiber (Figure 12, Plate VI). To economize space only a portion of the collateral *a* is shown in the figure, but in the preparation this collateral was traced into connection with a motor ganglion cell. *b*, one of the end branches of the collateral *a*, may be observed uniting with the small longitudinal fiber *d* at the point *c*. This fiber contains several neurofibrillae, while *b*, if not a single fibril, is composed of not more than two. *b* does not branch on uniting with *a*, but can be traced a short distance toward *s*, the anterior end of the longitudinal connective. In the preparation, *d* was seen to extend in both directions beyond the limits of the ganglion; naturally, its cell was not demonstrated, but the fact that it is much larger than *b* is sufficient ground for believing that all of the neurofibrillae which it contains do not come from the nerve element *a*. The connection between *b* and *d* at the point *c* seems as certain as if they were the branches of a single neurone.

Fibrillar Networks in the Neuropil.

A considerable number of cases of fibrillar networks occurring in the neuropil of *Hirudo* have been described in another paper (PRENTISS, 1903); two additional examples of the types which occur most frequently in *Hirudo*, are figured here. Often only two or three meshes are formed with which two or three fibrillae are connected (Figure 6, Plate V). In other cases the networks are much more complex, as seen in Figure 8. These examples were found near the center of the neuropil, and there is little likelihood of their being mistaken for networks in the cell processes. In every instance they were of limited extent, and comparatively few fibrillae were connected with them.

In *Astacus* more extensive networks may be demonstrated in the neuropil by means of methylen blue. Figures 9 and 13 are good examples of these fibrillar structures. The meshes

are larger than in the leech, and beads of perifibrillar substance are scattered along the course of the fibrillae, often at their points of union. These networks correspond more nearly to those which APÁTHY demonstrated in the leech with methylen blue, but they are not so extensive.

My observations thus confirm the statements of APÁTHY that fibrillar networks occur in both ganglion cells and neuropil. The evidence, however, does not support his view that the networks within the cells are formed by neurofibrillae which differ from each other in both structure and function. This conclusion is, moreover, in entire agreement with BETHE'S experiment which proved that the cells are not the centers of nervous activity as APÁTHY supposed. As to APÁTHY'S assumption of a diffuse fibrillar network in the neuropil, there is no evidence to show that such a condition exists. There are rather numerous small networks, each limited to a definite region in the neuropil, and putting comparatively few fibrillae into communication with one another.

Fibrillar structures in my preparations of both *Hirudo* and *Astacus*, confirm BETHE'S statement that many neurofibrillae are found in the nerve elements which are entirely independent of the ganglion cells. In *Hirudo all* the neurofibrillae of a nerve fiber may be put into communication with one another by networks before they enter the cell.

These facts all point to the existence of fibrillar continuity between the nerve elements; in both *Hirudo* and *Astacus* apparent cases of continuity between two neurones have been observed. Great weight cannot be laid on only two observations of such connection, for there is always the possible danger of optical error in tracing such exceedingly small structures. But the very existence of independent neurofibrillae in the nerve elements and the presence of fibrillar networks in the neuropil are incompatible with the idea that the nervous system is composed of anatomically independent, cellular units. On the contrary such conditions can be explained only by assuming that between the nerve elements fibrillar continuity exists.

The proof of such continuity does not, however, annihi-

late the neurone theory ; it simply modifies it. There is as yet no direct evidence to prove that these fibrillar networks in the neuropil may not be formed by the union of fibrils, each of which was developed in a distinct cell. At present we know nothing of the origin of the neurofibrillae in the central nervous system, and, therefore, the presence of independent fibrillae in the nerve elements does not necessitate the abandonment of the neurone idea ; for such fibrillae, which do not enter the cell, may be differentiated in the plasma of the cell processes, and be as much a part of the cell as the processes themselves. The fundamental experiment of BETHE ('98) while of great value to neurology, does not in itself prove the neurone theory false ; it merely shows that the nerve elements may function for some time without their cells; that the cells are not the batteries which generate the nervous current, as was formerly supposed.

An unprejudiced thinker can but agree with VERWORN (: 00) when he says that : "der Begriff des Neurons und damit auch die Neuronenlehre erst dann und nur dann erschüttert wäre, wenn es gelungen, zu zeigen, dass das, was wir als celluläre Einheit betrachten, in Wirklichkeit aus mehreren Zellen besteht." The only important evidence which at present goes to show that the "celluläre Einheit" of the nervous system "aus mehreren Zellen besteht," consists of BETHE's preliminary statements of his researches in the histogenesis and pathology of the nerve elements. Before passing judgment on BETHE's work we must wait until a full account of it appears. If, as is probable, the results of his work prove beyond a doubt that the supposed cell individual is the product of many cells, the neurone theory will be untenable. If not, the neurone theory will still remain—a *theory* ; for our present methods have thus far failed to prove "beyond a doubt," that the nervous system is made up of cell units, and nothing but cell units.

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EXPLANATION OF PLATES.

The fibrillar structures which are described in the text are reproduced by dark lines, as they appeared in the preparations; the outlines of the less important fibrils were drawn much lighter, for the sake of clearness. The Figures were projected and outlined with a LEITZ camera lucida (ABBÉ model). With the exception of Figure 10 the drawings were made with the use of a LEITZ 1-16 oil immersion objective, and a No. 4 ocular. With a tube length of 160 mm. and a projection distance of 320 mm. this system gives a magnification of approximately 2000 diameters. Figure 10 is magnified 160 diameters by means of a LEITZ objective No. 3, and ocular No. 4.

PLATE V.

All the figures are from toluidin blue preparations of *Hirudo*. Figures 2 and 3 are from material fixed in ether.

Fig. 1. An oblique section through a large ganglion cell and a portion of the neuropil, showing the connection between the fibrillae in the cell process. The greater part of the cell is cut away. *a*, *b*, two fibrillae from the longitudinal commissures; *c*, a short fibril connecting *a* and *b*; *d*, the bounding membrane between neuropil and ganglion cells.

Fig 2. A small ganglion cell with its process, portions of the peripheral fiber (*b*), and of two collaterals. Part of the peripheral fibrillar network is seen in the cell; in that region of the element, from which the collaterals branch off, a large fibril (*a*) may be traced from one of the collaterals into *b*, the peripheral fiber, where it is designated by *a'*.

Fig. 3. A ganglion cell of medium size from the same section as Figure 2. Only the neurofibrillae and the nucleus were visible in the preparation. *b*, the single large fibril in the cell process; *a*, one of its branches which unites with the network about the nucleus.

Fig. 4. A section through the peripheral portion of a giant ganglion cell, showing the close-meshed fibrillar network characteristic of the larger cells of *Hirudo*.

Fig. 5. A short portion of a cell process showing the connection between its neurofibrillae; *a*, *a'*, *a''*, three fibrillae which in passing from the cell into the neuropil, unite at *b*; at *c* a single mesh is formed, from which numerous small fibrillae continue their course in the process. The perifibrillar substance is not stained.

Fig. 6. One of the simpler cases of fibrillar networks found in the neuropil of *Hirudo*. Only two meshes are formed, which are in connection with three fibrillae.

Fig. 7. An example of the fibrillar networks in the processes of large nerve elements. *a*, proximal end of the cell process; *b*, bounding membrane of the neuropil; *c*, the network by which all of the fibrillae are connected together; *d*, a large neurofibril which unites at *e* with a smaller network.

Fig. 8. A fibrillar network of four meshes found near the center of the neuropil. *a-f*, fibrillae uniting with the network.

PLATE VI.

Figure 14 is a toluidin blue preparation from *Hirudo*. All the other figures are methylen blue preparations from *Astacus* material.

Fig. 9. A network of neurofibrillae from the third abdominal ganglion of *Astacus*. At the point *a* the network is apparently connected with the longitudinal nerve fiber *b*; *c*, beads of perifibrillar substance, characteristic of methylen blue preparations.

Fig. 10. A large motor nerve element from the second abdominal ganglion of *Astacus*. *a*, the enlarged portion of the fiber from which the collaterals branch off; *b*, the much smaller cell process; *c*, the peripheral nerve fiber, traced, in the preparation, to one of the lateral nerves; *d*, two collaterals. × 160.



C. W. P. DEL.



Heliotype Co., Boston.

Fig. 11. An enlarged drawing of that portion of Figure 10 from which the collaterals are given off. *b'*, *c'*, *a'*, correspond respectively to *b*, *c*, *d* in Figure 10. Many of the fibrillae do not enter the cell process; of these, *e* passes directly from one collateral to another.

Fig. 12. The collateral of a large nerve element which is apparently in direct connection with a longitudinal fiber. *a*, the collateral; *b*, the connecting fibril; *c*, its point of union with the fiber *d*; *e*, the anterior end of the longitudinal fiber *d*.

Fig. 13. A fibrillar network from the neuropil of the third abdominal ganglion; *a-f*, neurofibrillae which are connected with the network; *g*, beads of perifibrillar substance.

Fig. 14. One of the smaller ganglion cells of *Hirudo* (motor type of APÁTHY), showing the inner and outer fibrillar networks, which are put into connection by radial fibrillae.

Fig. 15. A ganglion cell from the last abdominal ganglion of *Astacus*. Only the fibrillae near the periphery of the upper half of the cell are shown.

ON THE INCREASE IN THE NUMBER OF MEDULLATED NERVE FIBERS IN THE VENTRAL ROOTS OF THE SPINAL NERVES OF THE GROWING WHITE RAT.

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This investigation is a continuation of previous work ('02) on the medullated fibers in the dorsal roots of the spinal nerves. The following results were obtained from the earlier investigation:

The spinal ganglia of the white rat were found to contain two kinds of cells which are differently characterized. One kind is of large size, while the other is much smaller. From the histological evidence, the larger cells were regarded as the adult functional form, while the smaller were considered to be the cells in a developing stage ('01).

If this view is correct and if the total number of cells in the ganglion remains the same throughout life, then we should expect more of the large cells in the ganglion of the adult than in that of the young animal. The converse should also be true; the younger animal should have more of the smaller cells in the ganglia. By counting the ganglion cells in animals of different ages, this hypothesis can be tested. According to Bühler ('98), the large functional cells are constantly degenerating, and the smaller cells which are developing take their place. If his view were true, the spinal ganglion cells should decrease in number as the animal gets older, since it is believed that in the rat the ganglion cells never divide after the first days of extra-uterine life. Bühler's hypothesis, therefore, can be tested by an enumeration of the total number of the spinal ganglion cells at different ages. For these two reasons, I undertook this investigation.

I enumerated the total number of the spinal ganglion cells and dorsal root fibers at different ages in several spinal nerves of the rat, and arrived at the following conclusions('02):

1. The total number of the spinal ganglion cells remains approximately constant between 10.3 grams (age 10 days) and 167 grams of body-weight (age 100 to 200 days).

2. All of the small cells contained in the spinal ganglia are constantly growing, and some of them become large cells. So that the number of large cells increases with age, while there is a corresponding decrease in the number of small cells.

3. The number of the cells in the spinal ganglia is always more than twice the number of medullated fibers in the corresponding dorsal nerve roots.

From the summary it is evident that the small cells are in a developing state and are becoming larger, while the fact that there is no numerical decrease in the total number of the cells favors my view, and is against that of BÜHLER.

In the present investigation the observation has been extended to the ventral root fibers. The method of preparation and the technique of counting were the same as used in the earlier investigation ('02). The following are the main results from this latter study:

TABLE I.

The Total Number of the Medullated Ventral Root Fibers in the Spinal Nerves Here Named.

	Weight of Rat 10.3 grms.	25.4	68.0	164.9	264.3	
Roots	VI Cerv.	558	1007	1302	1474	1522
	IV Thor.	286	434	561	613	772
	II Lumb.	333	698	704	1028	965
						Number of Medullated Nerve fibers.

As we see from Table I, the number of ventral root fibers steadily increases from 10.3 to 264.3 grams. The relative increase is nearly the same for the different nerves examined. Generally speaking, the total number of the medullated fibers in the adult animal is approximately 2.7 times that in the 10.3 gram rat, and the fibers increase most rapidly between the

weight of 10.3 and 25.4 grams, after which the increase is slower. In this respect the changes in the ventral roots are similar to those found in the dorsal roots.

Comparison of the number of the dorsal root fibers at 10.3 and 264.3 grams[1] indicates nearly the same rate of increase as is found for the ventral roots. The following table shows this:

TABLE II.

Relative Increase of the Medullated Dorsal and Ventral Root Fibers.

Weight of Rat	VI Cervical		IV Thoracic		II Lumbar	
	Dorsal	Ventral	Dorsal	Ventral	Dorsal	Ventral
10.3	1	1	1	1	1	1
264.3	2.0	2.7	2.9	2.7	2.9	2.8

As the table indicates, the total number of the dorsal root fibers of the 264.3 gram rat is about twice that of the 10.3 gram rat in the cervical region, while in the thoracic and lumbar regions the fibers are nearly three times as numerous. The different ratio shown between the three regions is probably due to the fact that the number of dorsal root fibers in the cervical region increases more rapidly between birth and 10.3 grams, than in the case of the two other regions. This special relation, however, should be further investigated.

A comparison between the number of the ventral and dorsal root fibers presents an interesting relation.

TABLE III.

Comparison Between the Number of the Medullated Ventral and Dorsal Root Fibers at Different Ages.

Weight of Rat.	10.3		25.4		68.0		164.9		264.3	
Root	Vent.	Dors.	V.	D.	V.	D.	V.	D.	V.	D.
VI Cerv.	558	1998	1007	2569	1302	3683	1474	4227	1522	4028
IV Thor.	286	607	434	863	561	1420	613	1522	772	1650
II Lumb.	333	723	698	911	704	1317	1028	1644	965	2102
Total Number	1177	3328	2139	4343	2567	6420	3115	7393	3259	7780
Ratios	1	2.9	1	2	1	2.5	1	2.3	1	2.3

[1] The observation on this animal has been made since the previous work ('02) was published.

For clearness, only the totals obtained by adding the fibers in the roots as shown in Table III, will be discussed.

As we see from the above table, the ratios between the two roots in 10.3 grams is 1:2.9, while in the mature animal it is 1:2.3. This means that the number of the ventral root fibers increases more rapidly than that of the dorsal root fibers, contrary to what appears in the frog (BIRGE, 1882). The addition of the new fibers between 165 and 264 grams is very small, and therefore the animal having a body weight of 165 grams may be regarded for this purpose as adult. These results show that the number of medullated fibers in the ventral roots of the spinal nerves of the rat as well as in the dorsal roots increase more than 100% with age—the age being indicated here by the body-weight. On the other hand, SCHILLER ('89), who counted the number of the medullated fibers in the oculomotor nerve of the cat at different ages, showed that the nerve of the new-born kitten contained 2942 fibers, while that of the eighteen months old cat was found to have 3035 fibers.

Thus, according to him, the number of the fibers added between birth and maturity was only 83; or hardly 3% more than the number found at birth. If this observation is correct, it indicates that the development of these efferent neurones in the cat is completed very early. The lack of accordance in the observations on the oculomotor nerve of the cat with those on the efferent spinal nerves of the rat, demands further study.

Several years ago, HARDESTY ('99), made the important observation on the spinal nerves of the frog that the number of medullated dorsal root fibers is more numerous near the ganglion than at the entrance of the dorsal root into the cord, while in the case of the ventral root, the number of medullated fibers diminishes from the cord towards the ganglion. This he interpreted to mean that the dorsal as well as ventral root fibers are growing (medullating) even in an older animal, and therefore as we pass away from the cells of origin, the number of mature fibers diminishes. DALE ('00), who counted the number of medullated fibers in the dorsal roots of several spinal

nerves in the adult cat, was not able to observe in that animal the numerical differences recorded by HARDESTY for the frog.

I have pointed out already, that the total number of the medullated fibers in the two roots increases from 10.3 to 264.3 grams, although the increase is not so marked between 65 and 264.3 grams as at the younger ages. From these facts, one might expect at the earlier ages an excess of fibers near the ganglia in the case of the dorsal roots, and near the cord in the case of the ventral roots, since the fibers are outgrowths of the cell-body located in spinal ganglion and ventral horn, respectively. In order to test this point, the fibers were enumerated at two levels in the ventral roots, one near the cord and the other farther from the cord and at the point where the ventral root approaches close to the ganglion, as had been done by HARDESTY in the frog, and the following results were obtained:

TABLE IV.

Numerical Difference of the Medullated Ventral Root Fibers of all three nerves, VI Cerv., IV Thor., and II Lumb., combined at the Two Levels, Proximal (near cord) and Distal (near ganglion).

Weight of Rat	10.3	25.4	68.0	164.9	264.3	
Proximal	1299	2244	2696	3169	3279	Number of the medullated fibers.
Distal	1177	2139	2567	3095	3259	
Difference	122	105	129	74	20	
or	9.4%	4.6%	4.7%	2.3%	0.6%	

As we see from the table, the ventral root in the proximal section, i. e., near the cord, contains more medullated fibers than appear in a more distal section. This difference at the two levels is greatest in the youngest animal (122 fibers or 9.4% in excess at 10.3 grams) and diminishes to 0.6% in the oldest rat examined. Since the difference decreases as the animal becomes older, we most readily explain the decrease of the difference by the growth of the fibers which at an earlier age are immature, and therefore stop short of the more distal section. We infer that even when the growth process stops, there are some fibers which are still incomplete and unfinished; this explains the fact that in the oldest rats differences are found

between the proximal and distal sections, although at this phase of the life cycle, the difference does not necessarily mean that growth in these rats is still taking place. Thus HARDESTY's observations on the frog are confirmed in the growing white rat.

Summary.

1. The total number of the medullated fibers in the ventral roots of the spinal nerves increases as the animal becomes older (Table I). The rate of increase of these fibers is not the same for the different ages. It is most rapid between the weights of 10.3 and 25.4 grams (10–30 days), after which it becomes slower. The number at maturity is about 2.7 times that found in the 10.3 gram rat.

2. The total number of the medullated fibers in the ventral roots in the 10.3 gram rat is approximately one-third of that in the dorsal root fibers (1:2.9), while in the adult the ratio is 1:2.3 (Tables II and III). Thus the increase of medullated fibers in the ventral roots is more rapid than in the dorsal roots.

3. At all ages, the ventral root near the cord contains more medullated fibers than appear more distally, the second section being taken near the ganglion of the corresponding dorsal root; in other words, the total number of the medullated fibers in the ventral root decreases from the spinal cord towards the periphery (Table IV).

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ON THE MEDULLATED NERVE FIBERS CROSSING THE SITE OF LESIONS IN THE BRAIN OF THE WHITE RAT.

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With Plate VII.

I. Historical Review.

The results of research on the regeneration of the neurones in the central nervous system of vertebrates have varied greatly according to the age and zoological position of the animals used for experiment. For this reason the observations found in the literature have been grouped for review according as they were made on amphibians, reptiles, birds, or mammals. It should be born in mind in considering this question, that regeneration in the central nervous system may involve either a proliferation of neurones as a whole, i. e., the growth of new elements resulting from cell division, or a restitution of parts of mature neurones which have been mutilated.

Spinal Cord of Amphibia.

In the spinal cord of amphibia the process has been described quite fully by Barfurth (**2**) (1891), who amputated the tails of frog larvae and was able to show that the cells lining the central canal became amoeboid and arranged themselves so as to close the canal. These cells then proliferated by indirect division, forming a tube which extended backward into the new tail. From this tube the new spinal cord with its ganglia and nerves developed. Fraisse (**12**) (1885) found a normally functioning cord in the regenerated tail of an amphibian larva. Harrison (**16**) (1898) secured results agreeing with

those of previous investigators, except that the spinal ganglia regenerated only in the most proximal part of the new-formed cord. SGOBBO (29) (1891) obtained positive results on frog larvae and tritons although the spinal cords of other vertebrates gave no evidence of regeneration.

The cases of the adult salamander and triton are very similar. CAPORASO (6) (1887), working with the latter animal, found that after cutting off part of the tail the spinal cord degenerated cephalad for a short distance, the cells lining the central canal remaining intact. These ependyma cells then proliferated, restoring first the degenerated area cephalad to the injury, and then extending backward to restore the part lost by the amputation of the tail. Within the new formed mass ganglion cells were differentiated. SGOBBO (29) and BARFURTH (2) have also reported positive results on the triton. MÜLLER (26) (1864) observed in the regenerating tail of the salamander a new cord, which resembled in appearance the lost part, but which did not establish functional connection with the new tail.

The results of work on the frog are much less conclusive. MASIUS and VANLAIR (24) (1869), after removing 2 mm. of the spinal cord of a frog, found that the cavity was subsequently filled with tissue containing what they took to be nerve cells and nerve fibers. Later MASIUS (23) (1880) reasserted his former conclusions, but as neither SGOBBO (29) (1891) nor MARINESCO (22) (1894) have been able to confirm his observations, it seems doubtful whether the spinal cord of the adult frog possesses even this degree of regenerative capacity.

In brief, all amphibian larvae and the adult triton can perfectly restore a lost portion of the spinal cord; the salamander accomplishes this only incompletely; and it is an open question whether the frog can do so at all.

Spinal Cord of Reptiles.

Lizards have been studied by MÜLLER (26) (1864) and FRAISSE (12) (1885), each of whom found the lost portion of the spinal cord partially reformed, but not so completely as to be of functional value. On the other hand, SGOBBO (29) (1891)

was unable to find any evidence of a regeneration of the spinal cord in these animals.

Spinal Cord of Birds.

Upon birds we have the observations of BROWN-SEQUARD (**4**) (1851), who severed the spinal cord in pigeons and subsequently found nerve cells and nerve fibers in the tissue joining the cut ends. In a paper published in 1892 he reaffirms his conclusions without further experimentation (**5**). SGOBBO (**29**) (1891) also experimented with birds, but failed to secure any evidence of regeneration. The observations on reptiles and birds are so few in number and so contradictory in character that no definite statement can be made. A further study of these forms would be desirable.

Brain of Frogs and Birds.

Much less work has been done on the brains of amphibia, reptiles, and birds. Two researches have been recorded in this field, each giving positive results, though neither has been confirmed. DANIELEWSKY (**9**) (1891) completely removed the cerebral hemispheres of a frog; and after nine months found a new cerebral mass, a microscopic study of which revealed cells which were believed to be nerve cells. VON VOIT (**35**) (1868) claims to have secured even more striking results on the pigeon. Five months after complete removal of the cerebral hemispheres in a young pigeon he found two new hemispherical masses, with a cavity in each. These masses, which were composed of nerve fibers and nerve cells, passed over into the crura cerebri. There has been no serious attempt to repeat these observations and they have neither been confirmed nor disproven. It would be profitable to apply to the study of the brains of the lower vertebrates the same methods that have been employed in the study of wounds in the brains of mammals, since there is nothing in this part of the literature to compare with the careful studies of COEN, SANARELLI, TEDESCHI and TSCHISTOWITSCH upon the mammalian brain.

It will perhaps be noticed that in this review the question of the restoration of function has been carefully avoided. This is because we are interested here only in the presence or absence of new-formed nerve elements, and this is a matter which can be studied quite apart from the physiological value of these elements. This restriction will make possible a clearer view of the literature on the regeneration of the spinal cord of mammals, which has been much confused by the failure to appreciate the difference between reflex and voluntary movements.

EICHORST and NAUNYN (10) (1874) crushed the spinal cord of dogs. In the connective tissue which developed in this region many nerve fibers were found. These resembled the fibers of peripheral nerves, from which EICHORST believes they are ingrowths. In one instance he was able to follow one of these fibers to a spinal ganglion. Since it was impossible to prove that all the fibers had been destroyed by crushing, these results were not favorably received. To meet this objection EICHORST (11) (1875) completely severed the spinal cord of several dogs and was able to confirm his previous results. The article published by MASIUS (23) in 1880 describes the removal of a part of the sacral cord in young dogs. Microscopic examination, made after healing had occurred, showed in the connective tissue many nerve fibers, mostly myelinated and grouped in bundles. These were continuous with the fiber tracts of the stumps. No nerve cells were found in the scar tissue. A month and a half after complete transection of the cord, STROEBE (30) (1894) found in the scar nerve fibers which had grown in from the dorsal roots. These fibers never completely crossed the line of the incision. He noticed a few mitotic figures in the ependyma cells lining the central canal, but could not show that they bore any relation to the scar formation. BAER, DAWSON and MARSHALL (1) (1899) report some careful experiments on dogs, which led them to believe, on the basis of physiological evidence, that the dorsal root fibers, which they had previously destroyed, had re-established

connections within the cord; but no microscopic examination was made.

A case of injury to the human spinal cord as a result of spinal fracture in the thoracic region, has been described by BORST and NICOLAIER (**3**) (1897). Here the scar contained numerous nerve fibers which were considered as ingrowths from peripheral nerves, that is, of course, from the dorsal roots.

It is worth noticing that fibers in the cicatrix are described by EICHORST, STROEBE, and BORST and NICOLAIER, as arising from the spinal ganglia, or, what amounts to the same thing, from the dorsal roots of the spinal nerves. This may also be inferred from the results of BAER, DAWSON and MARSHALL. Since it is known that the spinal ganglia always contain many undeveloped neurones (**17**), it is possible that these fibers are not regenerated fibers but represent neurones which have completed their development under the stimulus of the injury. KÜHN (**21**) (1901) has made an observation quite analogous to this. He found that depriving an area of skin on a frog's back of its sensory supply by sectioning one of the cutaneous nerves caused fibers to grow into that area from *uninjured nerves*. These, since they were not regenerating fibers, must represent axones which, being more or less incompletely developed before the experiment, have been stimulated to complete their growth as a result of the injury.

A large number of careful investigators have reported entirely negative results on the mammalian cord. SCHIEFFERDECKER (**28**) (1876) practicing transection of the cord in dogs a few months old, was unable to demonstrate any nerve fibers in the resultant scar. WESTPHAL (**37**) (1870) bored a small hole in the vertebral column and spinal cord but found no evidence of regeneration. KERESZTSZEGHY (**20**) (1892), SGOBBO (**29**) (1891) and MARINESCO (**22**) (1894) have also obtained negative results.

It will be seen that the evidence does not encourage the belief that the fiber columns of the cord are capable of regeneration, although fibers may grow into the scar from the dorsal roots. MASIUS, however, found fibers which seemed to arise

from the severed tracts of the cord. It seems that nerve cells in the injured spinal cord of mammals do not proliferate. The ependyma cells lining the central canal may show indications of mitotic division (STROEBE); which, when taken in connection with the observations of BARFURTH and CAPORASO on the regenerative capacity of these cells in the lower vertebrates, is of considerable theoretical interest.

Brain of Mammals.

The healing of wounds in the brains of mammals has been studied by numerous investigators, with a view to determining whether new nerve tissue is formed. TEDESCHI (31) (1897) has given a good account of the reaction of brain tissue to various injuries. Wounds were inflicted by him on the encephala of rabbits, guinea-pigs, cats and dogs, some by plunging a hot needle into the tissue, some by the introduction of a foreign body (a piece of paraffin) and others by resection of a large piece of a hemisphere. He also studied the effect of subdural injection of pathogenic bacteria. Three days after the introduction of a foreign body he observed at about 1 mm. distance from it a zone of reaction. Some of the nerve cells in this region were altered in form and contained vacuoles, fat droplets, and darkly stained nuclei. Many other nerve cells were in various stages of karyokinetic division. In isolated nerve cells he observed an abnormal arrangement of the chromatic substance of the nucleus, which might be interpreted as a phase in the dissolution of the cell. But there were also normally constructed karyokinetic figures, which resulted in cell proliferation. Mitosis was also seen in the neuroglia and endothelial cells. Some months after the operation the foreign body was surrounded by tissue, consisting chiefly of neuroglia but also containing a few ganglion cells and many nerve fibers. This nervous tissue is new-formed, he argues, because it is found in the place of tissue which had suffered profound degenerative changes. He also pictures a nerve cell which has sent processes between the lamellae of paraffin and which must therefore have been developed since the operation. When re-

section of a part of a hemisphere was practiced, the place of the excised tissue was taken by a soft reddish mass composed of nerve fibers, nerve cells and neuroglia. These statements would be more convincing if we could be sure that no nerve cells had survived the degenerative processes in the immediate vicinity of the foreign body; and that when a piece of the brain was excised, the margins of the wound did not become approximated, at the same time undergoing partial degeneration with glia formation, and thus giving rise to the soft reddish mass described as filling the wound.

Analogous to TEDESCHI's observations after excision of part of a dog's cortex, are the results of VITZOU (**33**) (1897) after ablation of the occipital lobes of a young monkey. About two years after the first operation he opened the skull again and in the second operation removed the tissue which was found occupying the position of the former occipital lobes. This mass, which he regarded as new-formed, was much the same in structure as normal brain tissue; but since it was removed under limitations imposed by the operation, neither its relation to the rest of the brain, nor its gross appearance was adequately described. Nor do his figures show the transition between the new-formed and the normal brain substance. For this reason one cannot be sure that it does not represent uninjured tissue displaced posteriorly. Whatever may be thought of the physiological evidence brought forward in this case, the anatomical evidence seems to be very inconclusive.

With regard to the mitotic division of nerve cells, TEDESCHI has received better support. FRIEDMANN (**13**) (1889) has observed that, when the irritation of the cortex is sufficiently severe and at the same time perfectly aseptic, proliferation of the ganglion cells may occur. MONDINO (**25**) (1886) and COEN (**8**) (1887) obtained similar results after puncturing the brains of guinea-pigs and rabbits with red hot needles. COEN, however, found that the new-formed ganglion cells soon disappeared, and the final cicatrix contained neither nerve fibers nor nerve cells.

While most of the investigators who have worked in this

field have observed mitotic figures in the nerve cells, not all agree that they result in cell proliferation. SANARELLI (**27**) (1891) used a hot needle on the cerebrum and cerebellum of rabbits. Three days later he found karyokinesis in the nerve cells, where it had not progressed in a normal manner, nor presented all the stages of true mitosis. At this time there appeared in the normal brain substance, elements resembling giant nuclei which he believes are the results of incomplete, atypical karyokinesis of the nerve cells. After eighty days the stab canal was filled with pure connective tissue, which was surrounded by a zone of neuroglia, and this in turn bordered on the normal brain substance. Nerve cells were not present in the connective tissue nor in the neuroglia formation.

MARINESCO (**22**) (1894) using the method of COEN and SANARELLI on the brains of young rabbits, guinea-pigs and cats, observed in the ganglion cells karyokinetic changes which did not, however, reach the "meta" stage. The cicatrix which formed later contained neither nerve fibers nor nerve cells. TSCHISTOWITSCH (**32**) (1898) found that brain wounds in young rabbits and dogs healed with pure connective tissue.

It is plain that nerve cells may begin to proliferate, sometimes not reaching the stage of metakinesis (MARINESCO), sometimes producing giant nuclei (SANARELLI), and at other times proceeding to cell division, with rapid disappearance of the new-formed cells (COEN). It is doubtful whether these new cells ever continue to exist, although they are reported to do so by TEDESCHI. It will be seen that observations have been confined largely to the nerve cells, the fibers receiving little attention.

Several investigations have been made upon scars from lesions in the human brain. WORCESTER (**38**) (1898) describes a case of complete degeneration of the right half of the corpora quadrigemina in a woman of 51 years. The region is filled with neuroglia. There are no nerve cells; but in the midst of the area is a much convoluted bundle of nerve fibers which appears to have grown in from the region of the red nucleus. ZIEGLER (**39**) (1876), KALDEN (**19**) (1891), and CHEN-

ZINSKI (7) (1902) have failed to find any nerve fibers or nerve cells in the scars resulting from wounds in the human brain.

II. Experimental Observations.

Introduction.

We know that not all the neurones are fully developed at birth. The number of undeveloped neurones in the young rat is especially large. Dr. ALICE HAMILTON has shown that mitotic figures are very abundant in the developing central nervous system of the white rat four days old(14). HATAI has shown that the number of nerve fibers in the dorsal roots of the spinal nerves of the rat increases steadily long after the animal is mature (17). The increase in the number of fibers in the dorsal roots he explains as due to the development of the small, non-functional cells of the spinal ganglion into large functional cells. He has been able to show that this transformation does occur (17). He has recently made similar observations on the ventral roots (18), showing also in accordance with the observations of HARDESTY (15) on the frog, that the number of fibers in the ventral root is greater in sections near the cord than in those at some distance from it. These observations indicate the presence in the ventral roots of nerve fibers that have not completed their growth. If we may infer the same method of growth in the central nervous system—and Dr. HAMILTON'S (14) observations would indicate that such an inference is justifiable—we may assume that new nerve fibers are constantly being formed in the brains of young rats and probably in the brains of other young mammals. The failure to find nerve fibers in the scar when young animals have been operated on involves, therefore, the conclusion that nerve fibers which would normally have developed through this region have failed to penetrate the cicatricial tissue. While it is not inconceivable that the dense fibrous tissue filling the wound should act as a barrier, it seemed probable that if sufficiently immature animals were used nerve fibers would be found crossing the site of the lesion. At the suggestion of

Professor DONALDSON, I undertook a series of experiments to test this hypothesis.

Technique.

For the purpose of this investigation young rats were especially suited, because of their immature condition at birth. According to a recent observation by WATSON (**36**) (1903) in this laboratory, the nervous system of the new born white rat does not contain a single medullated nerve fiber. During the first few weeks the increase in the weight of the brain is very rapid. For example, calculating from a series of records on the brain weight of the white rat collected by Professor DONALDSON, the youngest rat used in the investigation gained 500% in brain weight (from .2 g. to 1.0 g.) during the forty days following the operation. This increased weight is due in large part to the formation of new nerve fibers. We should expect that tissue undergoing such rapid development would react to an injury quite differently from that more nearly adult. Previous investigations have, however, been made largely on adult animals, or on those in a much later phase of development. Those used for this study were at the time of the operation aged respectively, No. 1, 21 days; No. 2, 7 days; No. 3, 3 days; No. 4, 0.5 days (12 hours).

The operation was very simple. A sharp-pointed thin bladed scalpel, 1 mm. in breadth, was passed through the soft skull and run 2 or 3 millimeters into the brain substance, far enough to cut through the corpus callosum. The wound was made in each case parallel to, and about 1 mm. to the left of the great longitudinal sinus and 2 mm. in front of the lateral sinus. These sinuses, which mark the medial and posterior boundaries of the cerebral hemispheres, are clearly visible through the membranous skull. They served as guides in making the operation, enabling one to cut into very nearly the same region in each brain. The operation consisted of a single stab, so producing a wound the shape and size of the end of the knife.

The usual aseptic precautions were observed; the instru-

ments were sterilized in boiling water; the site of the wound was freed from hair and washed in mercuric chloride, 1-1000. After the operation the opening was sealed with collodion.

It was not until many failures had been made that success was attained in raising the rats operated on during the first week of life. In the first cases when they were returned to the nest the mother ate them, and when fed by hand they could be kept alive for only a short time. Others working in this laboratory have experienced the same difficulty. It was supposed that the action of the mother was caused by some foreign odor clinging to the young rat after it had been handled. A certain degree of success, however, was secured by keeping the young in an incubator heated nearly to the body temperature, and forcing the mother, kept in a cage near by, to nurse them at regular intervals (every four hours during the day and eight hours at night). By this means some young were kept alive for ten days. It was found that as long as the young were kept warm the mother could safely be left with them and that after a time she would care for them of her own accord. It was also found that if the animals were taken from the nest under conditions which prevented the loss of body-heat, they could be returned to the mother with safety. For this purpose a jar was warmed to body temperature and filled with hot cotton. In this the rat was carried from the nest to the operating room, where it was placed in an incubator until all was ready. The rat was held in a hot cloth during the operation, which was performed in a few minutes and without anaesthetics. It was then returned to the hot jar and carried back to the animal room. When these precautions were observed the mother never refused to care for the young.

After the operation the rats were allowed to live for one month and a half. The brains were then removed, hardened in MÜLLER'S fluid at 40° C. for one month and imbedded in celloidin. The occipital region of each brain was cut in serial frontal sections 45 μ thick and stained by the PAL-WEIGERT technique. Also for comparison the brain of a rat, operated on at the age of four days and killed thirty-two days later, was

hardened in VAN GEHUCHTEN'S solution, imbedded in paraffin, cut in serial sections 6 μ thick, and stained in erythrosin and toluidin blue.

Results.

It will be most convenient to give a general description of the wounds in each of the four animals, and to follow this with a summary of the more important points as they are seen when the four specimens are compared. It will be found that this description differs from the usual accounts in the following points: (1) the absence of adhesions in the meninges, (2) the absence of a well defined connective tissue scar, (3) the atrophy of sectioned nerve fibers on the cell body side of the injury, (4) the distortion of the wound due to the shifting of areas in the growing cortex and (5) *the presence of nerve fibers crossing the site of the lesion.*

Rat No. 1 was operated on when twenty-one days old and was killed fifty-three days later. The wound was found in the occipital region of the left hemisphere, parallel to, and near the middle line. On examining the serial sections of this region the wound could be traced from near the posterior edge of the splenium forward for a little over 2 mm. In its anterior part it penetrates the cornu Ammonis and runs a slight distance into the thalamus. From this point the floor of the wound gradually slopes upward and backward until the surface of the cortex is reached. By reference to Fig. 1 the general character of the wound will be seen. It is visible as a light band running down from the surface of the cortex and extending just through the corpus callosum, but it does not at this point extend into the cornu Ammonis. Throughout its whole extent dark granular masses are apparent—the remains of unabsorbed blood. The scar tissue is quite abundant in this brain clearly marking off the wound from the normal brain substance. On comparing this preparation with a corresponding one in a set of serial sections of a normal rat brain, it was found that the banking up of fibers on the medial side of the wound is not entirely the result of the operation, as an evident excess of fibers on the

medial side is to be seen at a corresponding level in the normal brain. It happened that the knife passed along the line that forms the lateral limit of the medial area of dense fibers, and the presence of a band of scar tissue almost devoid of fibers enhances the contrast to some extent.

The light band which marks the path of the knife is almost devoid of fibers; but a few isolated ones may be distinguished in the scar. Although clearly visible in the original preparation, they do not appear in the photograph which was taken with a very low power. In order to show these more accurately than could be done by a drawing on a small scale, a camera lucida tracing has been made (Fig. 5.). This tracing was taken from the same preparation that was used for the photograph, and represents a point in the lesion one-third of the way from the corpus callosum to the surface of the cortex. This preparation is No. 27 in a series of 45 passing through this wound; it is therefore at some distance from either the anterior or posterior extremity of the lesion. These new formed fibers follow a very irregular course, so that it is not possible to trace them far in the plane of any one section. But in a number of cases it is possible to follow single fibers from the normal brain substance on one side through the scar tissue and into the normal brain substance on the other side. Such a fiber is seen in Fig. 5, *f*.

Thus two tests were rigorously applied before the conclusion was formed that the fibers in the scar were really new elements; 1st, The fiber in question must pass completely across the lesion, making connections with the brain tissue on both sides; and 2nd, The fiber must cross near the geometric center of the lesion. Fibers that passed into the scar and then back again into the brain substance on the side from which they emerged were not counted as new-formed, for these might have been displaced into the opening left by the knife. One could not be sure that they had been formed since the operation. Fibers that passed across the lesion near its anterior or posterior extremities or near its lower limit were also disregarded; for these might have been uninjured fibers crowded

into the degenerated areas. But a fiber such as is illustrated in the tracing, crossing the wound near its center and making connections with the brain tissue on both sides of the scar, must without doubt be new-formed.

Rat No. 2 was operated on when seven days old and killed forty-two days later. The wound in the skull was indicated only by a slight roughness, ossification at this point being as complete as elsewhere. The dura mater was normal and without adhesions to the scar in the skull or brain. The brain scar is not visible, its locality being indicated only by the arrangement of the surface veins which encircle it.

In serial sections the lesion is clearly defined for a distance of 1.5 mm., of which 1.2 mm. lies posterior to the line of the splenium. Throughout its whole extent the wound passes through the substantia alba of the occipital lobe, into the cortex covering its under surface. Scattered along through the white matter there is a considerable amount of unabsorbed blood pigment which was, however, largely absent from the section of which Fig. 2 is a photograph. As will be seen by reference to that figure, the cortex on the upper surface of the hemisphere has healed so completely that it is hardly possible to make out the path of the knife in the upper two-thirds of the grey matter, while in its lower third and in the substantia alba the lesion is clearly visible. Although the distribution of the fibers in the upper region of the cortex is quite normal, the knife must have passed through this area to have reached the structures below.

Somewhat lateralward to the wound in the upper part of the hemisphere is a peculiar aggregation of fibers in the cortex covering the ventral surface. This region is shown in more detail in Fig. 9. The dark granular masses indicate the line along which the knife has passed. Numerous fibers running downward from the white matter are seen to follow this line and on approaching the ventral surface to spread out in a fan-shaped area. Nerve fibers in considerable numbers may be seen crossing the site of the lesion. Especially is this noticeable just below the substantia alba (*f*).

It will be seen (Fig. 2) that the lines indicating the path of the knife above and below the white matter are not continuous, that below being more lateralward than that above, and running at a different angle. Since the injury was produced by a straight stab, this appearance can be explained only on the supposition that the areas of the cortex have shifted their relative positions during the process of growth. The shifting that takes place in the cortex over the corpus callosum is just the reverse, as seen in the sections near the anterior extremity of this same wound, where the part above the corpus callosum is more lateralward than the part below.

Rat No. 3 was operated on when three days of age and killed forty-one days later. No sign of the injury could be found in the skull or the dura mater. On the brain a pale pinkish groove, 1.5 mm. in length, marked the line along which the knife had entered the cortex.

When serial sections are examined, it is observed that the healing process is more complete than in the brains of the two older rats. The remains of unabsorbed blood are scarcely to be found; and at its anterior and posterior extremities the wound fades off so gradually into the normal brain substance that it is impossible by a study of serial sections to determine its exact limits. Its posterior extremity is slightly behind the end of the splenium, from which point it runs forward for a distance of a little more than 1.5 mm. By reference to Fig. 3 the general appearance of the wound will be seen. Lateral to the point of the lesion the corpus callosum has entirely disappeared from the injured region. A small portion of its fibers remains intact near the middle line; but elsewhere the substantia alba of the cortex rests immediately on the cornu Ammonis and the alveus. The alveus is absent for a short distance. The point near the middle line where the corpus callosum and alveus end represents the original position of the wound. By the large growth of fibers in the cortex medial to the lesion, the scar has been shifted lateralward until it has assumed the shape of a dilated V.

The disappearance of the corpus callosum lateralward to

the injury is of special interest. Had the sectioned fibers of the callosum merely degenerated in the part distal to the lesion, there would have been a considerable number of fibers in the corpus callosum on each side of the injury, instead of an entire absence of them on the lateral side. Their absence on one side and presence on the other can be understood by supposing that the fibers cut near their cells of origin—fibers whose cells were situated in the injured hemisphere—degenerated throughout their whole extent, while fibers cut at a greater distance from their cells of origin—fibers whose cells were situated in the opposite hemisphere—degenerated upon the distal side of the lesion only. In VON GUDDEN'S Gesammelte Abhandlungen (**34**) there is recorded a similar observation. Six or eight weeks after removal of one cerebral hemisphere in a young rabbit, he found that the anterior commissure and corpus callosum had completely atrophied in the remaining hemisphere.

In the upper region of the cortex the wound is recognized with difficulty, because there is so little scar tissue and the number of crossing fibers is so great. It can, however, be seen as a faint line along the path the knife must have taken to reach the underlying parts where the injury is more apparent. Fig. 6 is a camera lucida tracing of some of the fibers in the scar. It was taken from the same preparation as Fig. 3 about one-third the way up from the corpus callosum to the cortex. Two fibers fulfil the requirement of passing into the brain tissue on each side, and the others would probably do so if they could be followed far enough.

Rat No. 4 was twelve hours old at the time of the operation and forty days old when killed. The meninges were quite normal, and there was no sign of the injury apparent on the surface of the brain. Serial sections revealed a lesion extending 1 mm. behind the posterior extremity of the splenium and almost ½ mm. in front of that point. The general appearance of the wound is shown in Fig. 4. The upper part of the cortex is normal, no scar tissue can be seen there, and nerve fibers have a normal distribution. In the lower half is a trian-

gular area lighter than the rest, representing scar tissue that has taken the place of a large blood clot. This runs through all the sections, giving, when reconstructed, a mass in the shape of a three-sided prism with base directed ventrally. Below this lies the corpus callosum degenerated on both sides of the lesion. In this case the axons degenerated toward the cell whether cut before or after crossing the middle line. A few straggling fibers are seen in the otherwise unstained area. These probably represent neurones which have completed their development since the operation.

In the tissue composing the scar numerous nerve fibers pass in every direction interlacing to form a large meshed irregular network (Fig. 7). Fig. 8 is a camera lucida tracing of a part of this same area from another section of this brain. Owing to the unusual width of the scar in this region only a part of it could be represented in the tracing; the brain tissue along its margins is not indicated as in previous tracings.

The presence of medullated nerve fibers in the cicatricial tissue, demonstrated in each of the four brains, might be explained on either of two hypotheses. They might represent regenerated portions of nerve fibers cut by the operation; or they might have been formed since the operation by outgrowths from cell bodies incompletely developed at that time. Although there is nothing in the appearance of any given section to exclude the former theory, the latter seems the more probable. This conclusion is supported by the uniformly negative results obtained by those who have studied wounds in the brains of adult mammals; and by the fact that in the four cases given here the number of fibers in the scar diminishes regularly as the age of the animal at the time of the operation increases. (Compare Fig. 8 with Figs. 6 and 5). These facts might be explained as indicating a loss of the regenerative capacity of the neurones within the brain as the animal becomes older; but are more probably due to the diminution in the number of undeveloped cells capable of sending axons across the lesion subsequently to the injury. During the period of active growth with which we have to deal the diminution in the number of

these cells would be sufficiently rapid to explain the decrease in the number of the crossing fibers. An observation, which tells strongly against the regeneration theory in this case, is that the fibers of the corpus callosum degenerated toward their cells of origin after being cut in the two younger rats, while they remained intact on the cell side of the injury in older rats. This observation shows that nerve fibers instead of possessing unusual regenerative power in these young animals (where the largest number of nerve fibers were found in the scar) tend to degenerate completely after injury.

Summary.

(1). The adhesions which are described by other investigators as binding the brain scar to the meninges and the meninges to the tissue filling the skull wound were entirely absent in these young rats.

(2). Very little scar tissue was found in the brain. In the upper part of the cortex it was not noticeable in PAL-WEIGERT preparations; in the substantia alba it was more abundant. With the exception of the large triangular area in the brain of rat No. 4, there is a steady decrease in the amount of scar tissue with the decrease in the age of the animal at the time of the operation. How little connective tissue there is in the wound is seen in Fig. 10. Nerve cells quite normal in appearance border directly on the line that represents the path of the knife. Only here and there can a connective tissue cell be found in the scar (*c*). In the brains of older animals the connective tissue is very abundant at the site of the lesion. It may be that the absence of a dense connective tissue scar in the cases here given may in part explain the positive results obtained on the crossing of nerve fibers, but the increase in the number of nerve fibers is out of proportion to the decrease in the amount of scar tissue.

(3). A degeneration of the fibers of the corpus callosum toward their cells of origin was noticed in the two younger rats.

(4). Shifting of the parts of the cortex with reference to

each other occurred in all but the oldest rat. In rats Nos. 2, 3 and 4 it was found that the parts of the cortex had altered their relative positions in the same manner, such that if we consider the under surface of the cortex as stationery the cortex upon the upper surface shifts lateralward over the splenium, Fig. 3, and medialward in the posterior part of the occipital lobe, Fig. 2. This is explained by the fact that when a large number of fibers develops in any area, that area increases in size more rapidly than the surrounding parts. In Fig. 3 is seen a dense area of fibers just medial to the scar, which is responsible for the lateral displacement of the scar.

(5). We have seen that at the center of stab wounds, where every fiber must have been cut by the knife, medullated nerve fibers may be traced across the wound and into the normal brain tissue on each side. While there can be no doubt that these are new formed elements, they represent in all probability not *regenerated* but *entirely new* axons. The number of such fibers is very great in the youngest rats, but decreases quite rapidly as the age of the rat at the time of the operation increases. Unfortunately the brains of rats operated on at a more advanced age were spoiled in the process of hardening, and I cannot say at what time the brain of the rat ceases to have the capacity of sending fibers across the site of the lesion.

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EXPLANATION OF FIGURES.

PLATE VII.

Figs. 1–4. Photo-micrographs of frontal sections of the left cerebral hemispheres of rats, showing the position of the scar and the general appearance of the surrounding parts. Sections 45μ stained by the PAL-WEIGERT technique. The cut is indicated by "*c*". The scar is seen as a light band, medial to which the fibers are numerous, and lateral to which they are less abundant.

Fig. 1. From Rat No. 1, operated on when twenty-one days old and killed 53 days later.

Fig. 2. From Rat No. 2, operated on when 7 days old and killed 42 days later. Showing aggregation of fibers in the scar in the ventral part of the cortex just above the sharp notch on the ventral surface. Notice that the scar has been distorted by the shifting of the areas of the cortex with reference to each other.

Fig. 3. From Rat No. 3, operated on when 3 days old and killed 41 days later. Notice the complete disappearance of the corpus callosum lateral to the injury.

Fig. 4. From Rat No. 4, operated on when 0.5 day old and killed 40 days later. Notice the degeneration of the corpus callosum on both sides of the lesion.

Fig. 5. Camera lucida tracing of the fibers in and about a small area of the scar (Rat No. 1) seen in Fig. 1, taken at a point about one-third of the way from the corpus callosum to the surface of the cortex. The arrow indicates the path of the knife, and "*f*" a fiber crossing the scar.

Fig. 6. Camera lucida tracing of the fibers in and about a small area of the scar (in Rat No. 3) seen in Fig. 3, taken at a point about one-third of the way from the corpus callosum to the surface of the cortex. The arrow and "*c*" have the same significance as in the preceding figure. The fibers in the scar are slightly more abundant than in Fig. 5.

Fig. 7. Drawing of the area of scar tissue (Rat No. 4) seen in Fig. 4,

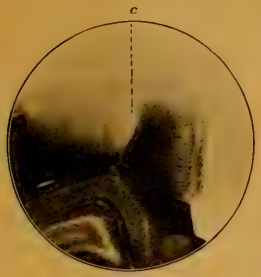


Fig. 1

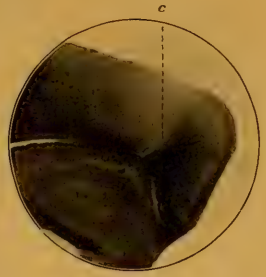


Fig. 3

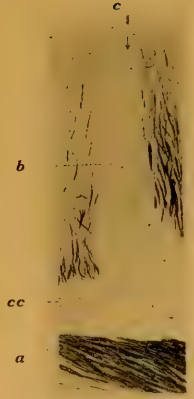


Fig. 7



Fig. 9

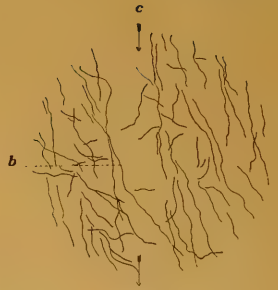


Fig. 5



Fig. 2

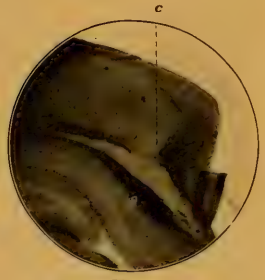


Fig. 4



Fig. 8



Fig. 10

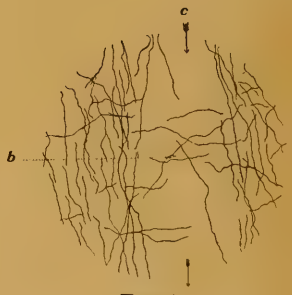


Fig. 6

made on a small scale because the scar was too wide to be included with the surrounding tissue in a high power tracing. The alveus (*a*) is normal. The corpus callosum (*c.c.*) is unstained, with the exception of a few fibers. The arrow indicates the path of the knife and "*f*" designates a fiber apparently crossing the scar.

Fig. 8. Camera lucida tracing of a small area of scar in another section from the same brain (Rat No. 4) as that represented ln Fig. 4.

Fig. 9. Drawing of the aggregation of fibers in the scar in the ventral part of the cortex (Rat No. 2) shown in Fig. 2. Notice the masses of blood pigment (*b*) along the line of the wound indicated by the arrow. Many fibers run downward along the scar, some of which cross the line of the incision at "*f*".

Fig. 10. Drawing from a frontal section of the left cerebral hemisphere of a rat operated on at the age of 4 days and killed 32 days later. The cortex was fixed in VAN GEHUCHTEN'S solution, imbedded in paraffin, cut in sections 6μ thick, and stained in erythrosin and toluidin blue. The path of the knife is indicated by "*c*". Notice the absence of connective tissue cells, and the presence of nerve cells bordering directly on the line of the incision.

ON THE DENSITY OF THE CUTANEOUS INNERVATION IN MAN.

By Charles E. Ingbert.

(*From the Neurological Laboratory of the University of Chicago.*)

I. Introduction.

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2. Estimate Based on Voischvillo's Results.
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VI. Summary.

VII. Bibliography.

I. Introduction.

It was, at first, the author's intention to publish this discussion as a part of his more extended paper on the "Enumeration of the Medullated Nerve Fibers in the Dorsal Roots of the Spinal Nerves of Man." This, however, was found im-

practicable owing to the accumulating evidence that STILLING's estimate of the number of nerve fibers in the ventral roots of the spinal nerves, which was used in calculating the number of cutaneous fibers in the dorsal roots, was not sufficiently accurate for our purpose. The data necessary for this calculation are the enumerations of the nerve fibers in both the dorsal and the ventral roots. The former the author has published (1903), as already mentioned. It was therefore necessary to make a similar enumeration of the fibers in the ventral roots. This being now completed, the estimation of the density of the cutaneous innervation in man is possible and is here presented.

II. The Relation of the Cutaneous and the Muscular Nerve Fibers of the Dorsal Roots of the Spinal Nerves of Man.

Having determined the number of nerve fibers in the dorsal roots of the left side in man (INGBERT, 1903), our next step is to inquire how many of these afferent fibers innervate muscles and other deep tissues, and how many the skin.

According to SHERRINGTON's (1894-95) observations on the cat, the afferent nerve fibers in a muscular nerve constitute two-fifths and the efferent three-fifths of its fibers. Or in other words, in a muscular nerve the afferent nerve fibers are to the efferent as 2 to 3. If we assume that this relation is typical of all muscular nerves, and if we assume that the same relation is true for man, then to the total number of efferent muscular nerve fibers, i. e., to the total number of nerve fibers in the ventral roots, there must be added two-thirds as many afferent fibers in order to make up the muscular nerves. In this calculation we have neglected the recurrent nerve fibers in the ventral roots because, even if present in man, their number must be very small. The fibers of the ventral roots passing into the white *rami communicantes* have also been neglected, because their number is not great and because we may assume without any serious error that the relation between the afferent and

efferent fibers in them does not differ sufficiently from that in other peripheral trunks to modify our result.

1. Estimate Based on Stilling's Results. According to STILLING (1859) there are in man, in round numbers, 500,000 nerve fibers in the dorsal roots of the spinal nerves of both sides, and 300,000 in the ventral. We therefore take from 500,000 fibers a number equal to two-thirds of 300,000, or 200,000 fibers, in order to add these to the efferent fibers in the muscular nerves. This leaves 300,000 or 60% of the nerve fibers of the dorsal roots to innervate the dermal surface of the body. If these data were correct, as unfortunately they are not, we could conclude that about 60% of the afferent fibers in the dorsal roots of man are cutaneous, i. e., go to innervate the dermal surface of the body, and about 40% go to the muscles. In the 60% credited to the skin there are included the fibers which pass to the viscera by the *rami communicantes* and recurrent nerves, if any, but so far as we know, the number of these is small, and, for the present purpose, may be neglected.

2. Estimate Based on Voischvillo's Results. Another calculation on the relation of the cutaneous and the muscular nerve fibers in the dorsal roots of man can be made from the results of VOISCHVILLO (1883) and those by myself. VOISCHVILLO sectioned the peripheral nerves in man at the places where they divide into cutaneous and muscular branches. The material used by him was hardened by 1% osmic acid and preserved in 95% alcohol. The areas of the cross-sections of the nerves (of which I can find no record) were obtained by two methods, (1) by dividing the volume (determined by weighing) of a piece of nerve by its length, (2) by projections of the cross-section made by means of a camera lucida.

In estimating the number of fibers in a peripheral nerve VOISCHVILLO counted all the nerve fibers of the section of the nerve that could be seen within a certain number of the squares of the ocular micrometer, and from this result he estimated the number in the entire cross-section.

VOISCHVILLO's average for the number of nerve fibers in the cutaneous nerves derived from the brachial plexus of one

side is 119,337. Since, according to my count, the dorsal roots (C. V.—Th. I) which help form the brachial plexus, contain 193,095 fibers, the cutaneous fibers in these roots as determined by VOISCHVILLO amount to 61.7%. In considering the dorsal roots C. V.—Th. I as the roots giving rise to the afferent fibers of the brachial plexus I have made use of P. EISLER'S drawings (Rauber 1893). According to these drawings the brachial plexus also receives a branch from the roots of C. IV and another from the root Th. II (N. intercostobrachialis). These two sources of gain would make VOISCHVILLO'S results too large were it not for the fact that he omitted in his estimate the cutaneous fibers given off by root Th. I in the N. intercostalis primus, as well as the few cutaneous fibers in the rami dorsales of C. V to Th. I. These two factors no doubt counterbalance each other to a great extent and thus justify us in our calculation

Again, by adding VOISCHVILLO'S averages for the number of nerve fibers in the cutaneous nerves derived from the lumbosacral plexus of one side, I find them to amount to 154,459 fibers (his own total, by another method which I cannot understand, is 82,167). According to my count, the dorsal roots (L. II—S. III) which help form this plexus contain 228,117 nerve fibers. In other words, according to VOISCHVILLO'S results 67.7% of the nerve fibers in these dorsal roots are cutaneous.

I have omitted the root L. I in this calculation because VOISCHVILLO made no estimate of the peripheral nerves derived from this root. The roots S. IV. S. V, and Coc. I, have also been omitted for the same reason. The gain from the root of L. I is, no doubt, counterbalanced to some extent by losses in branches passing into N. pudendus and N. clunium medius which he omitted.

3. Estimate Based on the Author's Enumeration. According to the author's enumeration (INGBERT, 1903) the left dorsal roots of the spinal nerves of a large man contain 653,627 medullated nerve fibers. Since the publication of this report the author has made an enumeration of the medullated nerve

fibers in the ventral roots of the spinal nerves of the same cord. This latter enumeration gives 203,700 medullated nerve fibers on one, the left, side of the body, or about 407,400 on both sides. (The report on this investigation will be published in the near future.)

As already mentioned, according to SHERRINGTON (1894–95) there are two-thirds as many afferent nerve fibers in a muscular nerve (a mixed branch to a muscle) as there are efferent fibers. We must, therefore, take two-thirds of 203,700 or 135,800 from 653,627 and add them to the efferent fibers in order to represent all the muscular nerves. This leaves 517,827 nerve fibers to innervate the dermal surface of the body; or, in other words, 79.22% of the fibers in the dorsal roots to innervate the dermal surface and 20.78% to supply muscles and other deep tissues with afferent nerves.

4. Comparison and Discussion. For comparison let us now repeat these estimates of the number of cutaneous fibers the in the dorsal roots:

1.	Estimate Based on STILLING'S Results	60.00%
2.	Estimate Based on VOISCHVILLO'S Results	
	a. Brachial plexus	61.70%
	b. Lumbar plexus	67.70%
3.	Estimate Based on Author's Results	79.22%

The low figure obtained from STILLING'S data is doubtless due to STILLING'S failure to include the fibers the diameter of which is less than 7μ, as the author has already demonstrated (INGBERT, 1903, p. 68), together with the fact that these fibers of a small diameter are more abundant in the dorsal roots, a point to be discussed in another paper. We consequently conclude that his figure for the number of fibers in the dorsal roots is more below the true one than his figure for those of the ventral roots. This becomes apparent on a comparison of the ratio between the fibers in the two roots.

	Ventral Roots.	Dorsal Roots.
STILLING	1	1.66
INGBERT	1	3.20

The cause of the low figure obtained from VOISCHVILLO'S

results is not so easily found; but is probably partly due to the fact that his results represent an estimate and not an enumeration. It is also highly probable that the osmic acid did not in the material used by him bring out all the smallest fibers sufficiently well to be included.

In order to determine the value of the calculations for the innervation of the skin about to be given, it will be well to consider in detail the methods by which the data for these calculations were obtained.

III. DETERMINATION OF THE AREA OF THE DERMAL SURFACE OF THE HUMAN BODY.

1. Krause's Determination. KRAUSE (1844) determined the dermal surface of the body to be 1,584,300 mm^2. or about 15 square feet. I can find no record of his method, nor any description of the subject used.

2. Funke's Determination. In making his determination of the area of the dermal surface FUNKE (1858) covered the half of a cadaver with gummed paper cut into one inch squares, as well as into smaller pieces, the values of which were determined beforehand. In so doing care was exercised to cover every part of the skin, to allow no overlapping of the paper, and to guard against the folding of either the paper or the skin. The results obtained he considers accurate within a square inch. He thus determined the areas separately for each part of the body, and gives as the entire area 1,651,700 mm^2.

3. Fubini and Ronchi's Determination. These investigators (1881) divided the surface of the body into its anatomical regions and marked these by sharp lines. These regions were then divided into such geometrical figures as could easily be measured. For the head a craniometer was employed. The measurements were made on the cadaver of a man 1.62 meters in height, and 50 kg. in weight. They determined the areas for the different parts separately and found the entire area to be 1,606,685 mm^2.

4. Meeh's Determination. MEEH (1879) combined in his method several valuable features. On large even surfaces he

marked the regions by red lines and traced these on transparent paper. These areas were then measured from the paper. Around the fingers he wound strips of paper of a uniform width. Other uneven surfaces he covered with gummed paper. Although MEEH measured several subjects, the results for a thirty-six years old man, corpulent, 171 cm. in height, and body-weight 78.2 kg., only are given.

Area for the right side of the body:

Head	80,380 mm².
Neck	45,660 "
Trunk	294,160 "
Upper arm	78,150 "
Fore-arm	67,860 "
Hand	53,850 "
Thigh	201,250 "
Shank	126,920 "
Foot	66,930 "
Pelvic region	106,580 "
	1,121,740 mm².

Both sides (his own figure) 2,243,490 mm².

By pelvic region MEEH means the dermal surface of the hips, i. e., the area between a line running along the crest of the pelvis and one transversely around the thigh about on a level with the *tuberculum pubicum.* This region is innervated by lumbar and sacral nerves and is included in the area for the the entire leg.

MEEH's line between the neck region and the trunk region runs from the top of the *acromion process* along the clavicle on the ventral surface of the body and on the dorsal surface to about the level of the spine of the seventh cervical vertebra. Since, however, the nn. *supraclaviculares* innervate a portion of the skin below the clavicle, it is probable that his area for the neck region is a trifle too small for the skin innervated by the cutaneous nerve fibers in the dorsal spinal roots C. I–IV.

5. Summary of Determinations of the Area of the Entire Dermal Surface of the Human Body of Adult Men.

Age	Height in Cm.	Body wt. in Kg.	Area of Dermal surface in mm².	Observer.
17 years, well-built	169	55.8	1,920,550	MEEH (1879)
20 years,	170	59.5	1,869,530	" "
26 years,	162	62.3	1,895,960	" "
36 years, corpulent	171	78.3	2,243,490	" "
36 years, emaciated	158	50.0	1,758,740	" "
45 years,	160	51.8	1,799,350	" "
66 years,	172	65.5	2,028,150	" "
(Not given)	?	?	1,584,300	KRAUSE (1844)
(Not given)	?	?	1,651,700	FUNKE (1858)
(Not given)	162	50.0	1,606,685	FUBINI and BONCHI (1881)

Having now data for the number of cutaneous nerve fibers in the dorsal roots of the spinal nerves of man, and for the area of the dermal surface of the body, we are enabled to make calculations as to the innervation of the skin, not only for the body as a whole, but also for some of its principal parts.

IV. THE INNERVATION OF THE DERMAL SURFACE OF THE HUMAN BODY.

1. Donaldson's Estimate. DONALDSON (1901) for the area of the dermal surface made use of the results obtained by MEEH for a man weighing 136 lbs.—1,900,000 mm². For the number of cutaneous nerve fibers in the dorsal roots he took 60% of STILLING'S estimate of 500,000,—300,000. According to this calculation, every cutaneous nerve fiber in the dorsal roots innervates, on the average, 6.3 mm². of the dermal surface.

2. Voischvillo's Estimate. This investigator (1883) outlined upon a cadaver the skin areas of the peripheral nerves as given by HENLE (1879).

These outlines were traced on transparent paper, and the area of these outlines determined by placing this transparent paper upon a sheet of paper ruled in sq. cm. and sq. mm. According to his summary there are 119,337 cutaneous nerve fibers to innervate the 130,084 mm². of dermal surface of the upper limb, or on the average one nerve fiber to every 1.1 mm². of skin; and 82,167 cutaneous nerve fibers (154,459

according to my addition of his results) to innervate the 303,566 mm². of the dermal surface of the lower limb, or on the average one cutaneous nerve fiber for every 3.7 mm². of skin. If my addition of his results be correct this will give one cutaneous nerve fiber to every 1.9 mm². of skin.

3. Author's Estimate. Since the cadaver from which the spinal roots used in my count of the nerve fibers was that of a man weighing 180 lbs. or 81.6 kg., I have made use of MEEH's data, as already given, for the heaviest man measured by him, one weighing 78.3 kg.

A. Body as a whole :

Area of one side of body,	1,121,740 mm².
Deduction for skin of the head innervated by the cerebral nerves, (⅔ of 80,360)	53,573 mm².
Corrected area,	1,068,167 mm².
Number of cutaneous nerve fibers (79.22% of 653,627)	517,827
1,068,167÷517,827=	2.05 mm².

Hence, every cutaneous nerve fiber in the dorsal roots innervates on the average 2.05 mm². of the dermal surface.

B. Arm :

Area of the arm,	199,860 mm².
Number of cutaneous nerve fibers in dorsal roots, C. V.—Th. I (79.22% of 193,095)	152,970
199,860÷152,970=	1.30 mm².

Hence, every cutaneous nerve fiber in the roots C. V—Th. I innervates, on the average, 1.30 mm². of the dermal surface of the arm.

C. Head and Neck :

Area of one side of neck,	45,660 mm².
Area of one-third of head on one side,	26,786 "
Total,	72,446 mm².
Number of cutaneous nerve fibers in dorsal roots of C. I.—IV (79.22% of 84,404)	66,865
72,453÷66,865=	1.08 mm².

Hence, every cutaneous nerve fiber in the dorsal roots of C. I—IV innervates, on the average, 1.08 mm². of the dermal surface of the neck, and that part of the head not innervated by cerebral nerves.

D. Leg:

Area of surface of one leg,	501,680 mm².
Number of cutaneous nerve fibers in the dorsal roots L. I—Coc. I (79.22% of 258,502)	204,785
501,680÷204,785=	2.45 mm².

Hence, every cutaneous nerve fiber in the dorsal roots L. I—Coc. I innervates, on the average, 2.45 mm². of the dermal surface of the leg.

E. Trunk:
Area of surface, one side, 294,160 mm².
Number of cutaneous fibers in the dorsal roots of Th. II-XII (79.22% of 117,626) 93,182
294,160÷93,183= 3.15 mm².

Hence, every cutaneous nerve fiber in the dorsal roots Th. II–XII innervates, on the average, 3.15 mm². of the dermal surface of the trunk.

For the purpose of comparison these results may be summarized as follows:

Average area of dermal surface innervated by one afferent fiber.

Body as a whole,	2.05 mm².
Head and Neck,	1.08 "
Arm,	1.30 "
Leg,	2.45 "
Trunk,	3.15 "

4. Comparison and Discussion. As already shown, DONALDSON'S estimate of the innervation of the skin is, on the average, one cutaneous fiber to every 6.3 mm². of the surface of the skin. Since this estimate is based on STILLING'S determination of the number of nerve fibers in the dorsal spinal roots, it is evident that the source of the difference between this estimate on innervation and my own is the fact that STILLING'S results are only 40% of mine. To show that DONALDSON anticipated that STILLING'S results would prove less than they should be, I quote his statement concerning them: "It seems probable that both these estimates (i. e., for the fibers in the dorsal and ventral roots) were too low" (DONALDSON 1901).

The difference between VOISCHVILLO'S results and my own is due chiefly to the fact that he used 130,084 mm². and 303,566 mm². respectively for the area of the dermal surface of arm and leg, while I used for the same 199,860 mm². and 501,680 mm². In other words, using equal values for the area

of the dermal surface, the estimates for the cutaneous innervation by VOISCHVILLO will be very nearly the same as that obtained by myself.

A study of the following tables makes this apparent:

Estimate by VOISCHVILLO.

Part	Dermal area in sq. mm.	Number of Nerve Fibers	Area of Dermal Surface innervated by one cutaneous nerve fiber.
Arm	130,084	119,337	1.1 mm^2
Leg	303,566	154,459	1.9 mm^2

Estimate by Author.

Part	Dermal area in sq. mm.	Number of Nerve Fibers	Area of Dermal Surface innervated by one cutaneous nerve fiber.
Arm	199,860	152,970	1.30 mm^2
Leg	501,680	204,785	2.45 mm^2

Estimate based on Number of Fibers used by VOISCHVILLO and area of dermal surface used by Author.

Part	Dermal area in sq. mm.	Number of Nerve Fibers	Area of Dermal Surface innervated by one cutaneous nerve fiber.
Arm	199,860	119,337	1.42 mm^2
Leg	501,680	154,459	2.25 mm^2

One factor, however, is not considered in this comparison, viz: VOISCHVILLO's observations being taken at the periphery of the body would tend to give him a high number of fibers owing to their branching. But as his estimate on the innervation (using the same dermal areas) is very nearly the same as that obtained by myself, it is likely that his estimate of the number of cutaneous fibers is too low. This agrees with the fact that the calculation of the cutaneous nerve fibers in the dorsal roots of the spinal nerves based on VOISCHVILLO's data, gives only 60 to 67% while that based on my own data gives 79.22%.

Concerning my own estimate for the innervation of the skin, it may be remarked that it is probable that in different persons the skin areas differ more than the numbers of nerve fibers in the dorsal roots of the spinal nerves, and since I have made use of the spinal roots of a large man and the largest area of the dermal surface on record, it is probable that if a

smaller subject were used for the determination of both the number of fibers and area of skin, the area of skin for each cutaneous nerve would be somewhat smaller.

V. THE BEARING OF THE AUTHOR'S ESTIMATE OF THE INNERVATION OF THE DERMAL SURFACE ON THE THEORY OF THE SPECIFIC ENERGIES OF NERVES.

It might be of interest to consider the bearing this estimate of the innervation of the skin has upon different theories as to the number of classes of nerve fibers that mediate the dermal sensations. If we assume with WEBER (1846) that impulses giving rise to sensations of heat, cold, pressure, and pain, pass over the same afferent cutaneous nerve fiber, then the above calculations will hold true, viz., one cutaneous nerve fiber, on the average, innervates 2.05 mm^2. of the dermal surface, giving all these forms of sensation to that area. If, on the other hand, we assume with FOSTER (1891) that there are four classes of afferent cutaneous nerve fibers, then this estimate will have to be so changed that one cutaneous nerve fiber of each class will innervate, on the average, 4×2.05 mm^2., or 8.2 mm^2. of the dermal surface. To specify more in detail, one cutaneous nerve fiber of each class will have to innervate 4×1.3 mm^2., or 5.2 mm^2. of the dermal surface of the arm; and 4×3.15 mm^2., or 12.6 mm^2. of that of the trunk. If this theory be true, then a histological examination of the nerve terminations in the skin ought to show each cutaneous fiber of the dorsal roots to innervate, on the average, an area of the skin of the trunk equal to 12.6 mm^2. However, until we know the amount of branching of these fibers, not only in the skin but also in the peripheral trunks, we are unable to judge whether or not it is possible for one nerve fiber to innervate so large an area of the skin.

VI. SUMMARY.

1. According to the estimate here made, about 79% of the medullated nerve fibers in the dorsal roots of the spinal nerves of both sides, or 1,032,730 fibers, go to innervate the dermal surface and about 21%, or 274,521, are afferent fibers

distributed to muscles and deep tissues. The afferent fibers of spinal ganglion origin passing in the *rami communicantes* are not separately considered in this estimate, but for the moment are classed with those passing to the skin.

2. According to my estimate (using the skin areas for a large man), one cutaneous nerve fiber in the dorsal spinal roots innervates, on the average, 1.08 mm^2. of the skin of the head and neck, 1.30 mm^2. of the skin of the arm, 2.05 mm^2. of the skin of the entire body, 2.45 mm^2. of the skin of the leg, and 3.15 mm^2. of the skin of the trunk; and for each additional class of nerve fibers assumed we must increase the area proportionately.

3. If we assume, with FOSTER, four classes of cutaneous nerve fibers, then each fiber will have to innervate, on the average, 4.32 mm^2. of the dermal surface of the head and neck, and 12.6 mm^2. of the dermal surface of the trunk.

4. If there be four classes of afferent nerve fibers in the dorsal roots of the spinal nerves of man, then a histological examination of the nerve terminations in the skin ought to show each cutaneous nerve fiber to innervate, on the average, areas of skin as large as given above.

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ON A LAW DETERMINING THE NUMBER OF MEDULLATED NERVE FIBERS INNERVATING THE THIGH, SHANK AND FOOT OF THE FROG—RANA VIRESCENS.

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During the past three years, while following the studies of Dr. Dunn (1900 and 1902) on the innervation of the frog's leg, it has been my endeavor to discover whether there was any law determining the distribution of the medullated nerve fibers to the segments of the leg. This law has been found and is expressed as follows:

The nerve fibers entering the leg of the frog (Rana virescens) by the sciatic and crural nerves, are distributed to the thigh, shank and foot in numbers which, for each of these segments are equal to the sum of the efferent fibers,—taken in proportion to the weight of the muscles,—and of the afferent fibers,—taken in proportion to the area of the skin.

The data discussed in the following pages are intended to furnish the evidence for the law just stated.

To make this investigation it was necessary to know:

(1) The relative number of medullated ventral and dorsal root fibers in the nerves supplied to the frog's leg.

(2) The relative weight of the muscles of the thigh, shank and foot.

(3) The relative areas of the skin for the thigh, shank and foot.

(4) The number of medullated nerve fibers entering the leg and also the number distributed to each segment.

(5) The number of medullated fibers distributed as muscular and cutaneous nerves to each segment of the leg.

With the exception of the data called for under (3), the facts needed were to be found in papers already published from this laboratory. We shall take up the points in the order just given.

(*1*) *The relative number of medullated ventral and dorsal root fibers in the nerves supplied to the leg.*

The nerves sending fibers to the leg are the VII, VIII and IX spinal nerves as usually numbered, or, according to the recent numbering of GAUPP (1897), the VIII, IX and X.

According to the enumeration of the medullated nerve fibers in the dorsal and ventral roots of these nerves by HARDESTY (1899, p. 84), the proportion is.

TABLE I.

	Relative number of fibers in roots, Ventral.	Dorsal.
Frog weighing 48 grams	100	177
" " 59 grams	100	175

The average of these two observations gives therefore 100 ventral root fibers to 176 dorsal root fibers, and this is the ratio here employed. Such being the relation found in the spinal roots, it is assumed to be the same in the sciatic and crural nerves at the point where they enter the leg. Whatever the number entering of fibers the leg, they are then to be divided, as motor and sensory, in the above proportion.

In this calculation no correction for possible efferent fibers in the dorsal roots is attempted, for we have no data with which to work. When efferent fibers appear in the dorsal roots of the frog, there is indirect evidence that the number must be quite small, and they are here neglected (HORTON-SMITH 1897, WANA 1898, DALE 1901). The ventral root is assumed, therefore, to contain only motor or efferent fibers and the dorsal root only afferent or sensory fibers.

Having determined the proportional numbers of the afferent and efferent fibers, the next step is to present the measurements according to which these fibers are to be distributed, namely, the relative weights of the muscles and the relative areas of the skin in the several segments of the leg.

(2) *The relative weight of the muscles of the thigh, shank and foot.*

In an earlier study, made in collaboration with Mr. SCHOEMAKER (1900) it was determined in Rana virescens that the relative development of the muscles of the frog's leg, as indicated by the weight of the muscles of the thigh compared with those of the remainder of the leg, was nearly constant for all groups above five grams in body-weight (see DONALDSON and SCHOEMAKER, 1900, pp. 124–125).

TABLE II.

Giving in grams the weights of the muscles in the thigh, shank and foot of the Frog—R. virescens. (From Table VII, DONALDSON and SCHOEMAKER, 1900.)

	Body			*Weight of Muscles*		
No	Sex	Weight	Lgth.	Thigh	Shank	Foot
18	F	29.40	185	3.105	1.141	.533
				3.097	1.201	.538
19	F	30.45	179	3.330	1.240	.659
				3.232	1.195	.603
20	F	33.96	172	3.480	1.393	.603
				3.681	1.354	.631
22	M	38.16	200	3.637	1.563	.715
				3.536	1.456	.653
23	F	42.54	215	4.455	1.562	.822
				4.369	1.535	.843
25	M	45.37	205	4.383	1.496	.869
				4.278	1.493	816
26	F	46.00	216	4.797	1.844	.926
				4.830	1.828	.926
27	F	47.58	206	4.713	1.741	.824
				4.616	1.813	.871
28	F	48.33	220	5.402	1.906	1 006
				5.430	1.949	1.019
29	F	52.55	206	5.404	2.450	.835
				5 456	2.400	.850

From Table VII, in that paper is taken the following series of records comprising numbers 18–29, inclusive, (excluding numbers 21 and 24 for which the muscle weights were not determined). This is the series just as it stands in the original table, and these same records have also been employed in my paper "On a Formula for Determining the Weight of the Central Nervous System of the Frog from the Weight and Length of its Entire Body," 1902.

For a description of the method by which the weights of the muscles were determined, the reader is referred to the original paper (p. 118).

For the first five frogs entered in the table, calculation gives the following proportional values for the weights of the muscles of the thigh, shank and foot:

TABLE III.

Segment of Leg	Percentage Value of Weight of Muscles.
Thigh	63.9%
Shank	24.3%
Foot	11.8%

In the case of the second five frogs in this same table, the proportional values are as follows:

TABLE IV.

Segment of Leg.	Percentage Value of Weight of Muscles.
Thigh	63.9%
Shank	24 5%
Foot	11.6%

It will be seen that these two series differ only by some tenths of a percent. in the case of the shank and foot, so that the relative values may be considered fairly constant.

For use in the present investigation we take the average of the two series which gives:

TABLE V.

Segment of Leg.	Percentage Value of Weight of Muscles.
Thigh	63.9%
Shank	24.4%
Foot	11.7%

Having obtained the data according to which the motor fibers entering the leg should be distributed, we need next to

obtain the corresponding data for the areas of skin,—in accordance with which the afferent fibers are to be distributed.

(3) *On the relative areas of the skin of the thigh, shank, and foot.*

Since the relative weights of the muscles in the several segments of the frog's leg remain unaffected by the size of the frog (DONALDSON, 1898, and DONALDSON and SCHOEMAKER, 1900), and since the conformation of the leg is similar in large and small frogs, it follows that the relative areas of the skin covering the different segments of the leg are unaffected by the absolute size of the frog examined. This removes the necessity of always working with frogs of the same size.

My acknowledgments are due to Dr. DUNN for working out the area of the skin in the several segments of the frog's leg. As the method used was somewhat novel, it will be necessary to describe it in detail.

The frogs examined had the following body measurements:

TABLE VI.

Frogs examined for area of skin.

Frog No.	Body Weight, grams.	Length from tip of nose to end of longes ᵗtoe.
1	34.76	190 mm.
2	36.75	195 mm.
3	28.17	187 mm.

The procedure was as follows: The frog was killed with chloroform and pinned out on a sheet of cork with the ventral aspect uppermost. One leg was extended and abducted so that it made an angle of about forty-five degrees with the longitudinal axis of the body. A strip of glass about 3 cm. wide and a few centimeters longer than the frog's leg, was then passed beneath it. The leg thus rested on this strip of glass and was in turn covered by a similar strip of the same size. On the upper surface of the latter a layer of tracing paper had been fastened by a drop of paste at each of the four corners. Rubber bands were next passed over the two strips of glass and the leg lightly compressed between them. Before putting on the covering strip, however, the foot was stretched so as to

exhibit the full extent of the web. For this purpose, threads were tied to the first, third and fifth toes, pulled taut and fastened by pins. The web was stretched until the second toe showed a tendency to curl up, and this reaction was regarded as indicating the normal extension of the web. When so extended, the general outline of the foot is that of a quadrilateral.

These adjustments having been made, it was determined by measurements taken between the two strips of glass, that their faces were approximately parallel. Next an outline, just outside the contact line of the upper glass with the skin of the leg, was made with a pencil on the tracing paper, starting from the uppermost part of the thigh on one side, and following around the entire outline of the leg to the uppermost part of the thigh on the opposite side. The upper limit between the skin of the body and that of the thigh was marked by the adjustment of the glass strips, and the levels of the knee and ankle joints respectively, were fixed by passing needles through these joints when preparing the leg for this examination. By drawing, therefore, a line across the tracing paper at these several levels, the outlines for the thigh, shank and foot were obtained. It was assumed that the outline on the dorsal aspect of the leg would be similar to the one found on the ventral aspect. To obtain the areas for the sides of the leg, the distance between the two glasses at the hip, knee and ankle was measured and the length of the curved line (the "coast line") forming the lateral boundary in the case of the thigh and shank, taken on each side, by means of a waxed thread applied to the outline. This gave the initial measurements for the calculation of the area of the skin of the thigh and shank. Concerning the foot we shall speak later.

To illustrate the determination of the area for a given segment, let us take the thigh. In this case we have the area marked on the tracing paper between the boundary separating the thigh from the body and that separating it from the shank. The content of this area was determined in square millimeters by means of a planimeter and then doubled so as to include the

corresponding area on the opposite side; to this sum was added the areas obtained by multiplying the length of each curved side (the "coast-line"), by a number equal to half the sum of the height of the side at the hip plus its height at the knee.

The sum of the four areas thus obtained was considered as the total area of the skin of the thigh. By following the same steps, the total area of the skin of the shank was found. On coming to the foot, however, the method of determining the area required to be modified in order to include the additional surface represented by the toes. The original outline on the tracing paper gave the area of one side of the foot projected on a plane surface, to which, when doubled, should be added the amount represented by the elevation of the toes and that due to the thickness of the tarsus.

To illustrate the method used, the following figure is given:

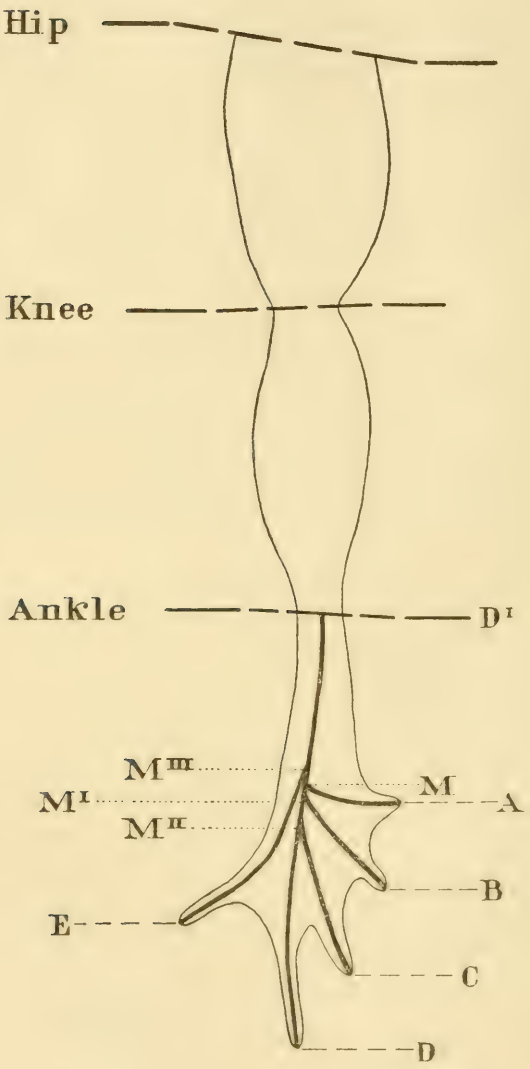


Figure 1. Outline of Frog's leg, showing the outline of the ventral aspect of right leg. *Hip*—marks the junction line of the body with the thigh. *Knee*—the junction line of the thigh with the shank. *Ankle*—the junction line of the shank with the foot. *D'–D.*—length of tarsus plus second toe. *M–A*—length of fifth toe. *M'–B.*—length of fourth toe. *M''–C*—length of third toe. (Second toe measured with tarsus). *M'''–E*—length of first toe.

The length of the line D'–D was first taken, then the thickness of the foot at D' and at D. Half the sum of these last two measurements multiplied into the length D'–D gave the lateral areas of the foot, considering these as extending from the ankle joint to the tip of the longest toe, and twice this gave the areas for both sides. The length of the lines MA, $M'B$, $M''C$ and $M'''E$ were then taken, and the thickness of the foot at M, M', M'', M''' and at each of the toes A, B, C and E (D being omitted, as it had been already measured). Half the sum of these two thicknesses was taken in each case as the average thickness of the toe, and the product of these numbers into the length of the respective toes, gave the area of the skin on one side of the toe considered as a plane surface. The surface is so rounded, however, that about one-half of the area thus calculated has already appeared in the surface projection of the foot, and has been counted in the area incluced within the original outline; therefore, intstead of taking this area for the side of the toes twice, it was taken only once.

Thus to get the total area for the foot, there are added together: the two areas from the tracing—the number of square millimeters being determined by the planimeter—the area for the longest toe including that for the sides of the tarsus and finally the additional areas for the four remaining toes.

The areas thus obtained for the three frogs measured are given in the accompanying table, the records for the two legs being entered separately.

TABLE VII.

Giving the areas in square millimeters of the skin covering the thighs, shanks and feet of three frogs—R. virescens. The method of measurement is given in the text.

	Areas in Square Millimeters.		
Frog.	Thigh.	Shank.	Foot.
1 Right	1584.1	1136.8	1695.3
1 Left	1675.5	1059.0	1793 6
2 Right	1519.2	1071.5	1539.1
2 Left	1506.3	1035.0	1538.7
3 Right	1377.0	1010.9	1396.5
3 Left	1356.2	972 4	1434.1
Totals	9018.3	6285.6	9397.3

When the percentage values of these numbers are found, they give the following:

TABLE VIII

Segment.	Average for first 3 entries	Average for second 3 entries	Average for all. 6 entries.
Thigh	36.5%	36.5%	36.5%
Shank	25.0%	25.8%	25.4%
Foot	38.5%	37.7%	38.1%

On attempting to apply these percentages in the calculation for the supply to the leg, it was found that the numbers obtained were somewhat larger than we expected them to be in the case of the thigh. It appeared that the area for the thigh had been over-estimated. Dr. DUNN therefore undertook a reinvestigation of the innervation of the skin of the thigh. This showed that the area was over-estimated in this sense, that in addition to the fibers entering the leg by the sciatic and crural nerves. there was a small independent bundle of nerves which entered through the anus and was distributed to a small triangle of skin just behind the anus and on the mesal surface of the leg. The area of this piece of skin thus innervated, was found to be 2.5% of the area of the entire thigh. For the details of this determination the reader is referred to a forthcoming paper by Dr. DUNN.

To control these results, other measurements were made by an entirely different method. A plaster mould of the frog's leg was taken and the leg then cast in WOODS metal. On this cast the thigh and shank were examined for their respective areas by winding them carefully with fine copper wire—of a uniform diameter. The diameter being constant, the areas covered by the wire would be directly proportional to the length or weight of the wire used. The relations were tested by weighing the wire. The weight of the wire needed to envelop the thigh, was to that needed to envelop the shank as 1.43 : 1.

On comparing this ratio with that from the areas for the thigh and shank, as shown in Table 7, it appears that this ratio is also 1.43 : 1.

Thus the proportional areas for the thigh as determined

by these two methods are identical. It would follow from this that the first method was probably accurate. On account of its shape the foot cannot be tested by this latter method.

When the area of skin for the thigh is reduced by the amount which is not innervated by fibers entering the leg in the sciatic and crural nerves, the following percentages are obtained as a general average from the three frogs measured:

TABLE IX.

Area of Skin.	
Thigh	35.9%
Shank	25.7%
Foot	38.4%

The above percentages are those used in the calculations which follow.

(*4*). *The number of medullated nerve fibers entering the leg and also the number distributed to each segment.*

Having thus determined the proportion in which the ventral root fibers and the dorsal root fibers entering the leg should be distributed to the several segments, it becomes desirable to estimate by means of the preceding tables, the total number of fibers going to each segment.

To show how this is done, let us assume that 100 ventral root fibers and 176 dorsal root fibers enter the leg—these numbers are in the proportion which has been determined. Then 63.9% of the 100 ventral root fibers go to the thigh and 35.9% of the 176 dorsal root fibers also go to the thigh. Now, in order to determine what percentage of the total 276, the sum of these two numbers is, we should divide their sum, namely, 63.9 fibers+63.2 fibers = 127 fibers by the total number of entering fibers, namely, 276. We then find that 46% of all the entering fibers go to the thigh when they are distributed in the above manner.

Extending the calculation in the same way to the shank and foot, we may tabulate the results as follows:

TABLE X.

Hereafter designated as the "formula".

$$\left.\begin{array}{l}46\% \text{ go to the thigh} \\ 25.3\% \text{ go to the shank} \\ 28.7\% \text{ go to the foot}\end{array}\right\} = 100\% \quad \left\{\begin{array}{ll}\text{shank} & 46.8\% \\ \text{foot} & 53.2\%\end{array}\right.$$

100.0% go to the leg.

If 46% go to the thigh, then 54% go to the remainder of the leg, i.e., shank and foot combined. Further, if we consider alone the fibers which go to the shank and foot and express the number as 100%, then of this 100% going to the shank and foot, 46.8% go to the shank and 53.2% to the foot. These calculations of the fibers distributed to the shank and foot are introduced here as they will be used later on.

The values in the above Table X are those with which all the subsequent calculations are made. It remains now to present the data concerning the number of nerve fibers observed to enter the leg of the frog and then to see in how far the estimated numbers for the segments of the leg correspond with the numbers which have been observed.

These observed numbers have been obtained by Dr. DUNN. The designation of the frog and the segment or segments for which the enumerations have been made, together with the date of publication, are given in the following Table XI in chronological order:

TABLE XI.

Frog B	Thigh	DUNN	1900
Frog C	Thigh	DUNN	1900
Frog B II	Thigh, Shank and Foot	DUNN	1902
Frog C II	Thigh, Shank and Foot	DUNN	unpublished

Below are given the details of the data for each frog so far as they will be required in this study.

The accompanying Figure 2, taken from Dr. DUNN's paper (1902), shows the levels at which the nerves for the frog's leg were sectioned and where the number of fibers was counted.

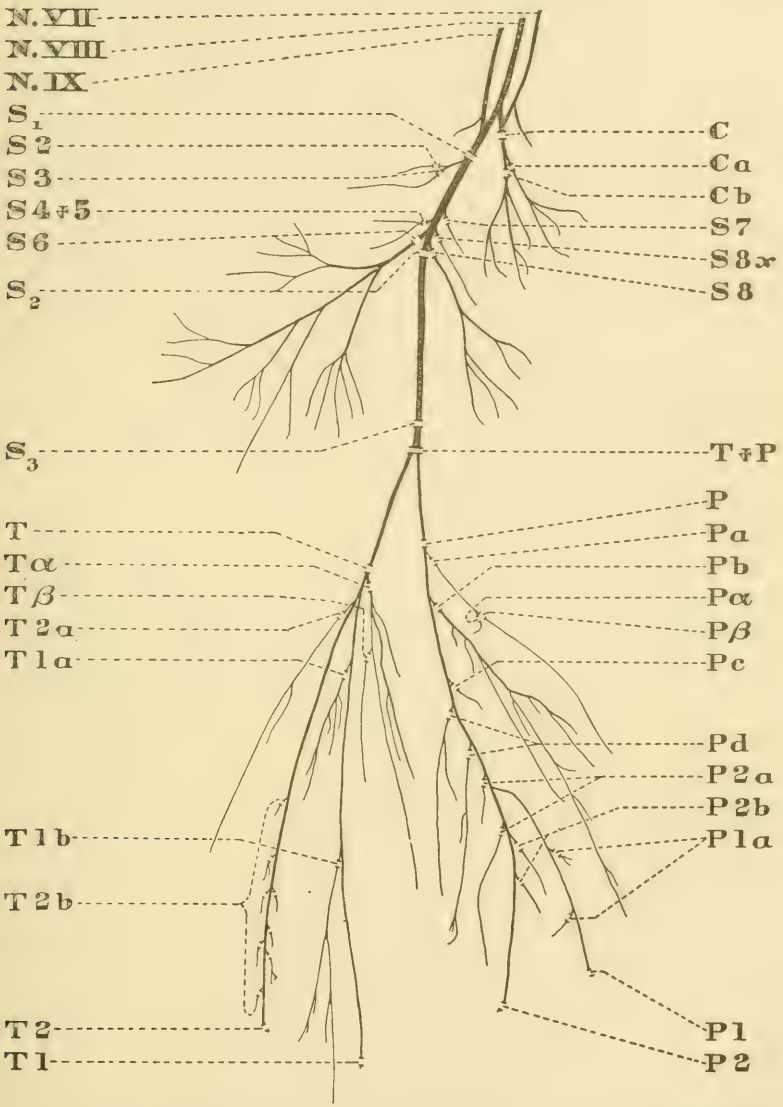


Figure 2. Diagram of the innervation of the Frog's Leg, showing the levels at which the number of nerve fibers was counted. *C*=level of Crural nerve just above branches to thigh. *S1*=level of Sciatic nerve just above branches to thigh. *S2*=level of Sciatic nerve just below branches to thigh. *P*=level of Peroneal nerve just above branches to shank. *T*=level of Tibial nerve just above branches to shank. *P1*, *P2*=level of Peroneal nerve just above branches to foot. *T1*, *T2*=level of Tibial nerve just above branches to foot.

Thus all the fibers entering the leg were in the sections at the levels $C+S_1$. All the fibers entering the shank were in the sections at P+T, and all the fibers entering the foot at P1+P2 and T1+T2.

In the Tables XII–XVI which follow, these designations are used to indicate the levels at which all the fibers for a given segment were to be found. Below the entry for the number of fibers to each of the segments, stands "To Thigh" and "To Shank," which means that all the branches to the thigh or to the shank contained the numbers there entered, under "observed." The number of fibers immediately below the branches to the thigh is also given after S_2.

In the column headed "muscular and cutaneous," are the observed numbers found in the muscular and cutaneous branches and their sum is equal to the "observed number" in each case.

In the column headed "calculated," we have the number determined by Dr. DUNN by taking the difference between the number just above the branches to the thigh ($C+S_1$), or shank (P+T), and the number just below at S_2 or at P1+P2 and T1+T2.

In the column marked "splitting fibers," we have the *difference* between the observed—the larger number—and the calculated—the smaller number—which difference is due to fibers that have split in their course so that they are represented either by two divisions having the same distribution (i. e., both run in the branches supplying the segment), or by one division running in the branches to the segment, and by the other in the main trunk of the nerve to some point below the level of the branches. It is the presence of these splitting fibers which renders complicated the application of the test which it is proposed to make, since the formula based on the law of distribution does not take account of the additional fibers which appear as the result of splitting.

TABLE XII.

Data taken from Dr. DUNN's paper, 1900; Tables III, IV, V and VI.

Frog B. *Right Leg.*

Locality	Number of Fibers			
	Observed		Calculated	Splitting Fibers
	Total	Cutaneous = C Muscular = M		
C + S_1	5273	------	------	------
To thigh	2623	C 876 M 1747	2405	218
S_2	2868	------	------	------

Left Leg.

C + S_1	5385	------	------	------
To thigh	2600	C 871 M 1729	2411	189
S_2	2974	------	------	------

TABLE XIII.

Data taken from Dr. DUNN's paper, 1900; Tables III, IV, V and VI.

Frog C. *Right Leg.*

Locality	Number of Fibers			
	Observed		Calculated	Splitting Fibers
	Total	Cutaneous = C Muscular = M		
C + S_1	6011	------	------	------
To thigh	2814	C 1279 M 1535	2643	171
S_2	3368	------	------	------

Left Leg.

C + S_1	5987	------	------	------
To thigh	2777	C 1219 M 1558	2586	191
S_2	3401	------	------	------

TABLE XIV.

Data taken from Dr. DUNN's paper, 1902; Tables V to XIV inclusive.

Frog B II. *Right Leg.*

Locality	Number of Fibers			
	Observed		Calculated	Splitting Fibers
	Total	Cutaneous = C Muscular = M		
C + S_1	7107	------	------	------
To thigh	3508	C 1678 M 1830	3165	343
S_2	3942	------	------	------
P + T	4152	------	------	------
To Shank	2130	C 1003 M 1127	1665	465
P1 + P2 and T1 + T2	2497	------	------	------

TABLE XV.

Data taken from Dr. DUNN's paper, 1902; Tables V to XIV inclusive.

Frog B II. *Left Leg.*

Locality	Number of Fibers			
	Observed		Calculated	Splitting Fibers
	Total	Cutaneous = C Muscular = M		
C + S_1	7129	------	------	------
To thigh	3481	C 1676 M 1805	3167	314
S_2	3962	------	------	------
P + T	4146	------	------	------
To shank	2108	C 903 M 1205	1660	448
P1 + P2 and T1 + T2	2486	------	------	------

TABLE XVI.

Data from specimen of R. virescens. Body-weight 51 grms. Observations by Dr. DUNN not previously published. The section at S_1 of the left leg was unfortunately too imperfect to be counted.

Frog C II. *Right Leg*

Locality	Number of Fibers: Observed	Calculated	Splitting Fibers
	Total { Cutaneous = C; Muscular = M		
C + S_1	{ 1301 C; 4610 S_1		
	5911 ------	------	------
S_2	3313 ------	------	------
P1 + P2 and T1 + T2	2026 ------	------	------

Left Leg

C + S_1	{ 1323 C; ------ S_1 (Section lost)		------	------
S_2	3389	------	------	------
P1 + P2 and T1 + T2	1969	------	------	------

To illustrate the use of the data in the foregoing tables, we will take the right leg of Frog B II (Table XIV), and determine how far the observed numbers there given agree with those estimated by the aid of my own formula. Table XIV shows 7107 fibers entering the leg. When the proportional numbers are calculated according to the formula (Table X), we obtain the following:

TABLE XVII.

Entering right leg of Frog B II—		7107 fibers
To thigh—	46.0%=	3269 fibers
To shank—	25.3%=	1796 fibers
To foot—	28.7%=	2042 fibers

The above numbers of fibers are the *numbers of single pathways between each segment of the leg and the entering nerve.*

When the observed numbers of fibers to the several segments of the leg (see Table XIV) are compared with those here estimated, we obtain the following:

TABLE XVIII.

Number of fibers to the several segments of the right leg of Frog B II.

	Estimated (DONALDSON)	Observed (DUNN)
To thigh	3269	3508
To shank	1796	2130
To foot	2042	2497

Thus in every case the numbers estimated by the formula are less than those observed by Dr. DUNN. But as Table XIV shows, Dr. DUNN'S count includes a large number of fibers which have split (see "splitting fibers" in tables), and which, therefore, are not taken into account by the formula, which applies to single pathways only.

The next step, therefore, in the comparison is to bring the two series of numbers to the same standard. There are two ways of doing this, namely, either by removing the additional fibers due to splitting from the number observed by Dr. DUNN, or by adding the additional fibers to the number as determined by the formula. The latter method was followed; first, because it was desirable to consider the *observed* number as the fixed standard, not to be altered in any way, and second, because it seems probable that the most direct utilization of this formula will be for determining the number of fibers which a direct count would show to be supplied to a given segment.

Thus in the further work, the observed number is in each case taken as the standard, and the calculations are directed to determining the number which must be added to that estimated by the formula in order to make it comparable with the standard. To illustrate the steps taken for this purpose, we shall do best to examine the innervation of the thigh in the case chosen, namely, the right leg of Frog B II. My estimation gives for the thigh 3269 fibers and Dr. DUNN'S observation 3508. When, however, in this instance the number of fibers observed *above* the branches to the thigh at ($C+S_1$) was diminished by the number observed just *below* the branches at (S_2), the difference was found by Dr. DUNN to be 343 (see Table XIV). Thus her observed number exceeded her number calculated in this manner by 343 fibers. This excess is explained as the

result of splitting fibers and means—if dichotomous splitting be the form assumed—that 343 of the fibers counted at $C+S_1$ have split later into two divisions each. Just where this splitting occurs, we are obliged to guess. The numerical results indicating the number of splitting fibers would be the same, whether it occurred in the main stem, $C+S_1$, just where the branches to the thigh are given off, or within the branches after these had been given off, but before the levels at which they were individually sectioned. For the further development of our idea of the innervation of the leg, however, these two possible arrangements leading to like numerical results, have very different values. In the latter instance, where the splitting occurs within the branches, the splitting fiber is in no wise represented in the main trunk of the nerve below the level of the branches, whereas in the former instance, where splitting occurs in the main trunk, one division can appear in the branches and the other continue in the trunk, the original fiber being therefore still represented in the trunk, below the point at which it has split.

It was necessary to assume that some of the fibers that split did so in the trunk, and thus were represented both in the branches and in the trunk below the branches, while others split in the branches themselves; both divisions in this case having a similar distribution.

After several tests, it was found that the most accordant results were obtained when it was assumed that one-third of the splitting fibers split in the branches. Fibers splitting in this way form Class a. Since the total number of splitting fibers was in this case 343, one-third would be 114.3 fibers. These are to be added to the number estimated by me (see Table XVII): $3269+114.3=3383.3$.

The number of fibers that pass to the shank and foot is not affected by this process, since each one of these fibers splitting in the branches is without representation in the trunk below the level of the branches.

By this step 114.3 of the splitting fibers have been with-

drawn from the original 343, leaving 228.7 to be still considered.

These remaining fibers are assumed to be of the second class of splitting fibers (Class b), i. e., those, one division of which passes into the branches, while the other continues in the trunk below the branches.

Since by the formula we have taken 46% of the total number of the fibers entering the leg (see Table XVII), we must assume that we took 46% of the fibers with double representation (Class b). It follows, therefore, that in the original 46% or 3269 fibers, there are already included 46% of the fibers with double representation, or 46% of the 228.7 fibers which constitute Class b at this level. Therefore, to bring the estimated up to the observed number in this respect, there are still to be added to the estimated number 100%—46%=54% of 228.7, which equals 123.5 fibers. In general, therefore, to make the estimated number comparable with that observed by Dr. DUNN, we should add one number representing the fibers splitting in the branches (Class a), and also a second number representing the splitting fibers with double representation (Class b), in so far as they have not been included in the original 46%.

TABLE XIX.

Showing the number of fibers to be added to the original 46% in the case of Frog B II—Thigh.

	Calculated numbers.	Observed number
Original 46%	= 3269	
Fibers splitting in branches (Class a)	= 114.3	
Splitting fibers with double representation (Class b)	= 123.5	
	3506.8	
	or 3507	3508
Difference	= 1 fiber	

As the table shows, the estimate is almost identical with the observation, being but one fiber less. Without commenting on this result at this place, we shall pass on to the consideration of the nerve supply to the shank of this same leg.

It must be kept clearly in mind that our calculation for the

percentage distribution of the fibers to the segments of the leg applies to the number of *single medullated fibers found entering the leg at* $C+S_1$; in this case, 7107 fibers. Having removed 46% of this number for the innervation of the thigh, there remain 54% to be distributed to the shank and foot.

Thus: 7107—3269=3838 fibers.

The law calls for a distribution of this 54% of the initial number in the proportion of 25.3% to the shank and 28.7% to the foot. When, however, we attempt to deal with the splitting fibers belonging to the shank and foot in making the estimated comparable with the observed results, it is necessary to distribute these splitting fibers in the same proportions in the branches to the shank as they were distributed in the branches to the thigh, and in order to make the distribution in a like manner, it is necessary to treat the number of fibers going to the shank and foot, 3838, as 100% of all the fibers concerned, and then designate those to the shank as 46.8% of the same number,

Since 46.8% of 3838=25.3% of 7107=1796

53.2% of 3838=28.7% of 7107=2042

According to the formula, therefore, 1796 fibers (single pathways) are estimated as going to the shank. Dr. DUNN observed 2130 fibers to the shank, and further, by the same methods as were employed in the case of the thigh, she determined that there were 465 splitting fibers in the branches to the shank. (See Table XIV.)

In adjusting the estimated number to that observed, these splitting fibers are treated in the same manner as those found in the supply to the thigh, i. e., one-third are taken as dividing in the branches, and of the remainder it is assumed that 46.8% are included in the original estimate, so that 53.2% only need to be added to bring the estimate to the same standard as that of the observed number. Thus, imitating Table XIX, for the thigh, we have the following:

TABLE XX.

Showing the number of fibers to be added to the original 25.3% in the case of Frog B II—Shank.

		Calculated numbers.	Observed number
Original 25.3% of 7107 or 46.8% of 3838	=	1796	
Fibers splitting in branches (Class a)	=	155	
Splitting fibers with double representation (Class b)	=	165	
		2116	2130
Difference	=	—14 fibers or 0.6%	

The approximation between the estimated and observed numbers is not so close here, but is still fair, being within less than one per cent.

The number of fibers to the foot has still to be considered. In the case of the foot, the observed numbers are taken from the enumeration at the levels P1+P2 and T1+T2. Figure 2. These levels would correspond to those just above the branches in the case of the thigh and shank. We have to assume, therefore, that in the number observed by Dr. DUNN at these levels as going to the foot, there are in addition to the single pathways represented by fibers that pass unsplit from their entrance into the leg, two other classes, those namely (a) that have split within the trunk, both divisions descending to the foot, and (b) all other split fibers, one division of which goes to either the thigh or shank, while the other goes to the foot.

Of the class (b), there are in the entire leg at least three groups: b_1, the fibers which split, one division passing to the thigh and the other to the foot; b_2, fibers which have split, one division going to the thigh and the other to the shank; b_3, splitting fibers which have one division going to the shank and one to the foot.

These several groups are all marked, Figure 3, as in b_1, b_2, b_3. At the level where the nerves enter the foot, it is necessary to make allowance for groups b_1 and b_3 of class (b), as well as for representatives of class (a).

According to formula, 2042 fibers pass into the foot. Dr. DUNN observed 2497. To make the estimated number comparable with that observed, the allowance for the splitting fibers

must be introduced. The principle involved in making the allowance is that the division of any splitting fiber which has already been counted as a fiber entering the leg is to be considered as additional, and hence added to my estimate of the number to the foot.

For example, the splitting fibers included in the original 46% of those entering the leg and sending one division to the thigh (b_1) are pictured as sending the other division to the foot.

This group (b_1) contributes 106 fibers to the foot. As the fibers representing these divisions have already been accounted for, they would not appear in my estimate, and hence must be added to it. In like manner, the long divisions of the splitting fibers which go to the shank come from fibers already counted and are therefore additional; thus these also should be added to my estimate. The latter group (b_3) represents 46.8% of the splitting fibers which pass to the shank and these amount to 145. To the original estimate of 2042, therefore, 106+145=254 is to be added, making a total of 2293 fibers. This number is still 204 fibers less than the observed 2497. The difference may justly be credited to the splitting fibers of class (a), namely those, both divisions of which have a like distribution. That many such splitting fibers occur is shown by Dr. DUNN'S observations (1902, p. 314).

The arrangement of the fibers as here imagined is exhibited in Figure 3, which is purely a schema. Here the largest column represents the fibers going to the thigh, the next largest those to the foot and the smallest those to the shank. The size of the columns is proportional to the number of fibers they contain.

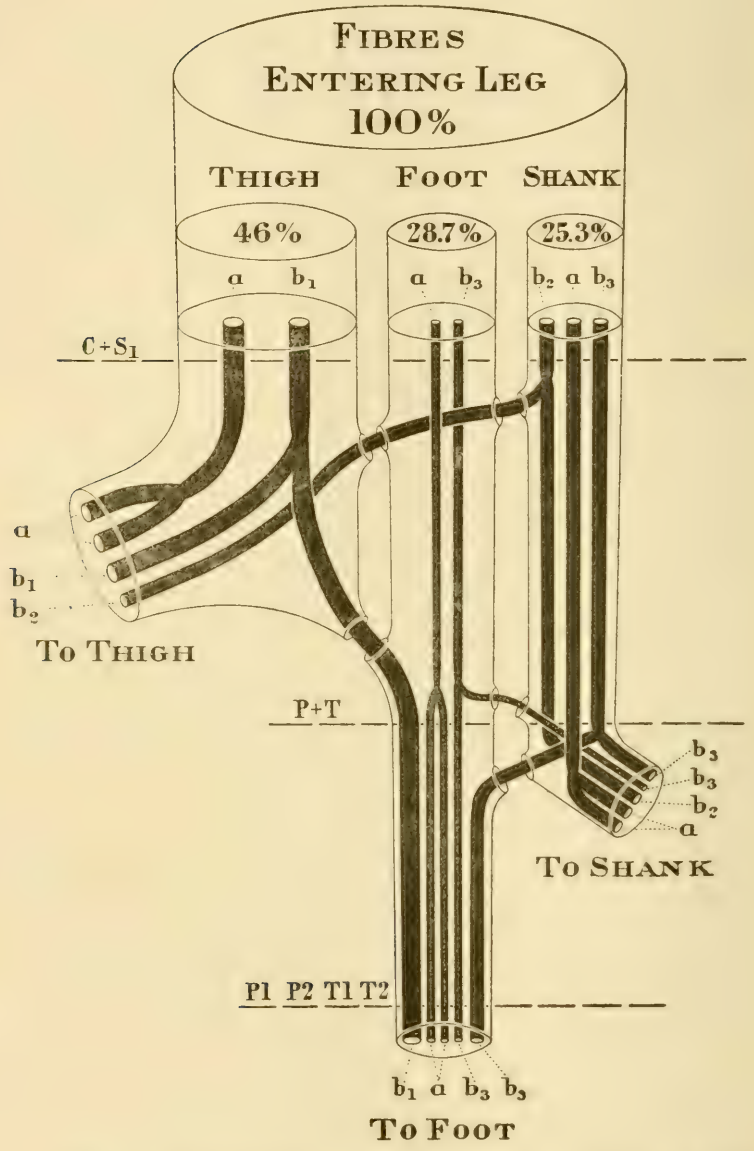


Figure 3. The explanation of this schema intended to illustrate the arrangement of the splitting fibers distributed to the leg of the frog, is given on the following page.

All the fibers entering the leg by the crural and sciatic nerves are enclosed within the circle marked "Fibers entering the leg, 100%." At the next lower level, the small circles enclose all the fibers to each of the three segments of the leg marked respectively:

Thigh 46.0%
Shank 25.3%
Foot 28.7%

Within the last three columns the heavy black lines indicate the splitting fibers, which according to the description in the text, are distributed to the the thigh, shank and foot. These splitting fibers are divided into two classes:

Class a—splitting fibers, both divisions of which are distributed to the same segment:

Class b—splitting fibers, the divisions of which are distributed to different segments.

This latter class is represented by three groups:

b_1, one division of which goes to the thigh and the other to the foot;

b_2, one division of which goes to the thigh and the other to the shank;

b_3, one division of which goes to the shank and the other to the foot.

$C + S_1$, indicates the level above the branches to the thigh; $P + T$, the level above the branches to the shank, and $P1 + P2$ and $T1 + T2$, the level above the branches to the foot.

Within each column is represented the several sorts of splitting fibers, each one bearing the designation used to indicate it in the text. The designation "a" always indicates the splitting fibers, both divisions of which have the same distribution. Class "b" is represented by the three groups, b_1, one division of which goes to the thigh, while the other goes to the foot; b_2, one division of which goes to the thigh and the other to the shank, and finally, b_3, one division of which goes to the shank and the other to the foot. The splitting fibers are counted only once, and are credited to the column in which they appear above $C+S_1$ in the figure. The other divisions are in addition to the number of fibers called for by the formula.

The levels C+S_1, P+T, and P1+P2 and T1+T2 are all indicated. If there were no splitting fibers the schema would be made up of the outlines of the three columns alone.

Turning now to general results of this test, we find that in the case of the right leg of Frog B II, the estimated numbers agree very closely with those observed when an allowance, *according to a fixed procedure*, is made for the splitting fibers.

The significance of this result depends largely on the possibility of repeating it. Using exactly the same methods, the results for the left leg of this frog (data presented in Table XV) are almost as good as those for the right.

The following table presents the results for both legs Frog B II:

TABLE XXI.

	Estimation (DONALDSON) Corrected for splitting fibers	Observed (DUNN)	Difference in fibers	Percentage
Thigh R	3507	3508	— 1	—.03%
Thigh L	3497	3481	+16	+.40%
Shank R	2116	2130	—14	—.65%
Shank L	2110	2108	+ 2	+.09%
Foot R	2497[1]	2497	----	------
Foot L	2486[1]	2486	----	------

[1] 8% of the observed numbers being added to represent the splitting fibers with a similar distribution of both divisions—see text.

This is the only frog we have in which the enumeration at different levels has been complete enough to permit of this full test of the formula. In Frog C II, however, the endeavor was made to determine whether the proportional distribution of the fibers at different levels in the leg would correspond with those found in Frog B II, for it seemed very probable that if the two frogs corresponded in this respect, they would also correspond in the number of fibers supplied to each segment of the leg.

The data for Frog C II give the number of fibers entering the leg at C + S_1 the number at S_2, and the number entering the foot, at P1 + P2 + and T1 + T2, see Table XVI.

On adding these three numbers together and then taking the proportional value of each of them, we find the following:

TABLE XXII.

Level	Right Leg	Left Leg
$C + S_1$	52.4%	------
S_2	29.4%	------
$P1 + P2 + T1 + T2$	18.2%	------

This calculation could not be repeated for the left leg, as the sections for S_1 were imperfect. The remaining sections were, however, counted at levels C, S_2 and $P1 + P2 + T1 + T2$ on the left leg, and gave numbers so closely similar to those from the right leg, that it is highly probable that the innervation of the two legs agreed closely.

The tabulation of these same numbers in Frog B II is given below:

TABLE XXIII.

	Right Leg	Left Leg
$C + S_1$	51.6%	51.8%
S_2	30.2%	30.1%
$P1 + 2\,P1 + T1 + T2$	18.2%	18.1%

When we compare these percentages with the corresponding determinations for Frog B II, in which the two legs are quite similar, we find that C II has .8% more in the thigh, .8% less in the shank and that they exactly coincide as regards the foot.

If we may judge from this, then other frogs are similar to B II in the general arrangement of the nerve supply to their legs, and hence the formula would be applicable to them as a class.

In support of this view, we have the results of applying the formula to Frogs B and C. In these cases to be sure, both legs were examined, but the supply to the thigh alone was observed and therefore the comparison is limited to that segment of the limb.

As the data for these calculations is to be found in Tables XII and XIII, it will be necessary to give only the comparison of the estimated number of fibers in each case with those observed.

TABLE XXIV.

	Estimation (DONALDSON) Corrected for the Splitting fibers	Observed (DUNN)	Difference	Percent.
Frog B				
Thigh r.	2577	2623	— 46	—1.7%
Thigh l.	2608	2600	+ 8	+0.3%
Frog C				
Thigh r.	2884	2814	+ 70	+2.5
Thigh l.	2887	2777	+110	+4.0

If we take the differences between the estimated and observed number of fibers to the thigh in all three frogs, B, C and B II, we find that the total is 251 fibers, neglecting signs, or deducting the — fibers from the + fibers, an excess of + 189 fibers. In the first case the difference amounts to an average of 1.4%, neglecting signs, or +1.1% when the signs are taken into account.

This is a very satisfactory approximation of the estimate to the observed number.

In the case of the shank we have only the two observations on Frog B II, with which to make the test. Here the approximation is closer, being 16 fibers when the signs are neglected, or a difference of — 12 fibers regarding the signs. This gives the percentage values of .37% and —.28%. In the case of the foot, owing to the fact that we have not the data for controlling the splitting fibers, the divisions of which have a similar distribution, but credit the differences between the estimated and observed numbers to this class, the test of the approximation cannot be made, as it has been for the thigh and shank. However it will be well to point out the reasons in detail for thinking that in the nerves to the foot, this class of fibers will account for the differences which have been found.

In the first place, Dr. DUNN (1902, p. 315, Table XII) has shown in Frog B II, between S_2, just below the branches to the thigh and T and P just at the entrance of the trunk into the shank, an interval from which no branches are given off—, that at the lowest level on the right side there was a gain of 210 fibers and on the left, 184, or 5.3% on the right and 4.5% on the left, the percentage in each case being based on the number

at S_2. This is proof positive of the splitting of the fibers within the nerve trunks. Moreover, in our calculations which were made to get the estimated number of fibers going to the thigh, the average value of the splitting fibers of class "a" in these case was 2.9%. For the two shanks of Frog B II it was 9.2%, while that demanded for the foot was 9.9%, all these percentages being based on the calculated number of unbranched fibers to each segment.

The significance of the foregoing paragraph is the following: When we assume the splitting fibers of this class to this amount, the results of the estimation and observation agree closely, and that in the shank where good agreement is obtained, we have assumed 9.2% of these splitting fibers, whereas in the foot, at which level our results cannot be tested in the same way, but where we should expect a priori a somewhat greater number of splitting fibers of this class, we are compelled to assume only a slightly greater proportion, namely 9.9%.

The claim made, therefore, for the splitting fibers at this level of the foot has ample indirect evidence in its favor.

Just at this point it may be fitting to call attention to the fact that the law here enunciated is deduced from the results already presented in four different investigations: HARDESTY (1899), DONALDSON and SCHOEMAKER (1900), and DUNN (1900 and 1902), that these were all independent and undertaken without any thought of the present problem, and that the data taken from them have been here employed without any modification whatsoever. The only special investigation taken up after this problem was formulated was the study of the areas of skin in the several segments of the leg, and the observation by Dr. DUNN on the nerves in Frog C II, with a view to testing whether the results on Frog B II might be considered as generally applicable.

This examination of the data from which the deduction has been made goes a long way to protect it from the criticism of bias, either unconscious or otherwise.

It has then been possible to show that, allowing fo

splitting fibers, the number going to any segment of the leg, calculated on the basis of the proportional area of skin and the proportional weight of the muscles, agrees very closely with the number observed.

To generalize these results, it is desirable to know, not only what percentage of all the fibers which enter the leg goes to any segment, as given by the formula in Table X, but also the percentage of that number that should be added to the supply of a given segment, to make it equal to the observed number.

This can be obtained by tabulating in each case the estimated and observed numbers, finding the number of fibers by which they differ and the percentage value of this number on the basis of the number estimated.

The averages of the percentages in each case then show the proportion of fibers which should be added to the estimate in order to represent the number which would probably be observed.

TABLE XXV.

Showing the percentage of the estimated number of fibers to be added in order to make the estimate agree with the number observed.

Frog	Estimate 46%	Added in calculation	Required to balance
		Thigh	
B. r.	2426	151 = 6.2%	197
B. l.	2477	131 = 5.3%	138
C. r.	2765	119 = 4.3%	49
C. l.	2754	133 = 4.8%	23
B II. r.	3269	237 = 7.2%	239
B II. l.	3279	228 = 7.0%	212
Total	16970	999 5.9%	858 = 5.0% Difference = .9%
		Shank	
	25.3%		
B II. r.	1796	320 = 17.8%	334
B II. l.	1802	308 = 17.1%	306
Total	3598	628 = 17.5%	640 = 18% Difference = 0.5%
		Foot	
	28.7%		
B II. r.	2042	455 = 22.3%	455
B II. l.	2048	436 = 21.3%	436
Total	4090	891 = 21.8%	891 = 21.8% Difference = 0%

A glance at Table XXV shows (1) that to make the 46% of the fibers entering the leg equal the number that will probably be observed to the thigh, 5% of itself must be added to it.

(2) That to make the 25.3% of the fibers entering the leg equal the number that will probably be observed to the shank, 18% of itself must be added to it.

(3) That to make the 28.7% of the fibers entering the leg equal the number that will probably be observed to the foot, 21.8% of itself must be added to it.

By the aid of these results, therefore, if one is given the number of fibers entering the leg, it is possible to estimate with a high degree of accuracy, the number which will be found going to any segment.

(5) *The number of medullated fibers distributed as muscular and cutaneous nerves to each segment of the leg.*

The efferent nerve fibers in a given segment are present in numbers proportional to the weight of muscle and the afferent according to the area of skin. The muscular nerves must contain all the efferent or motor medullated fibers, but it would certainly be very unexpected to find that the cutaneous nerves contained all the afferent fibers.

The number of cutaneous and muscular fibers has been determined in every instance for both thigh and shank by Dr. DUNN, and with this we can compare the distribution, calculated on the assumption that all the afferent fibers have a cutaneous distribution.

In the following table, in each instance, the calculated sensory (afferent supply, Cal. S.), is compared with the observed cutaneous (Obs. Cut.) supply—the calculated number always being the *larger*. The absolute difference in number of fibers is noted and its percentage value given—the number forming the observed cutaneous supply, being taken as a standard in calculating the percentage. In like manner, the observed muscular (Obs. Mus.) supply is compared with the calculated motor (Cal. Mot.), the observed muscular supply always being the *larger*—the absolute difference in number of

fibers as well as their percentage values are also given, the observed number being taken as the standard.

The shank is tested in the same way. For the foot observations are lacking. A study of the table will show, first, that the afferent or sensory fibers going to the muscles of the thigh are from 45% to 3.8% of the number of the cutaneous nerve fibers, while the excess of the muscular nerves of the thigh over the calculated number of motor fibers, is from 25.1% to 3.1% of the muscular nerve fibers.

In the case of the shank, the calculations for afferent fibers going to the muscles gives from 52% to 37% and an excess of fibers in the muscular nerves of from 34.3% to 38.6%.

TABLE XXVI.

Comparing the calculated number of sensory fibers with the number observed in the cutaneous supply and the calculated number of motor fibers compared with the number observed in the muscular supply and giving in each case the number of fibers by which they differ as well as the percentage value of this number. The observed numbers being used as the standards.

Frog	Thigh			Difference Cutaneous Abs.	%	Muscular Abs.	%
B. r.	Cal. S 1281	Obs. Cut. 876		405 =	—45.0%		
	Obs. Mus. 1747	Cal. Mot. 1296				451 =	+25.1%
B. l.	Cal. S. 1297	Obs. Cut. 871		426 =	—48.9%		
	Obs. Mus. 1729	Cal. Mot. 1311				418 =	+24.2%
C. r.	Cal. S. 1436	Obs. Cut. 1279		217 =	—17.8%		
	Obs. Mus. 1535	Cal. Mot. 1451				107 =	+ 6.8%
C. l.	Cal. S. 1434	Obs. Cut. 1219		145 =	—11.3%		
	Obs. Mus. 1558	Cal. Mot. 1450				85 =	+ 5.5%
B II r.	Cal. S. 1743	Obs. Cut. 1678		65 =	— 3.8%		
	Obs. Mus. 1830	Cal. Mot. 1763				67 =	+ 3.6%
B II l.	Cal. S. 1748	Obs. Cut. 1676		72 =	— 4.3%		
	Obs. Mus. 1805	Cal. Mot. 1749				56 =	+ 3.1%
	Shank						
B II r.	Cal. S. 1376	Obs. Cut. 1003		373 =	—37.0%		
	Obs. Mus. 1127	Cal. Mot. 740				387 =	+34.3%
B II l.	Cal. S. 1371	Obs. Cut. 903		468 =	—52.0%		
	Obs. Mus. 1205	Cal. Mot. 739				466 =	+38.6%

From these data it appears probable that in all these frogs and in every segment of the leg, some afferent fibers are distributed, with the muscular nerves. Moreover, the proportion thus distributed is shown to be very variable in the case of the thigh.

On comparing the proportion of these afferent fibers going to the muscles in the case of the shank, we find that the number is relatively larger than to the thigh. The comparison in the case of the shank B II, should be made, not with the data for the thighs of all the frogs, but with the data for the thighs of frog B II. Thus, in round numbers, there are in this instance, 4% of these afferent fibers to the thigh and 45% to the shank.

The better supply of the muscles with afferent fibers as we pass to the more distal segments of the limb, is what we should expect a priori, though in this case the difference appears very large.

Conclusions.

The present study is concerned with the number of medullated nerve fibers going to the different segments of the frog's leg.

1. The nerve fibers entering the leg being considered as so many separate lines of connection with the several segments are found to be distributed in accordance with the law that the efferent fibers are present in proportion to the weight of the muscle, and the afferent in proportion to the area of skin.

2. When this statement is reduced to numerical terms, it is expressed by the following formula:

Of the fibers entering the leg of the frog,

46.0% go to the skin and muscles of the Thigh.
25.3% go to the skin and muscles of the Shank.
28.7% go to the skin and muscles of the Foot.

3. Since some of the fibers split after entering the leg, the numbers found in the nerve branches to the segments are larger than the number of single pathways assigned to the segment by the formula. Calculation shows that to determine the number which will probably be observed in each case, the

number given by the formula must be increased by a certain percentage of itself:

For the Thigh by 5.0%
For the Shank by 18.0%
For the Foot by 21.8%

4. When due allowance is made for the splitting fibers, it is found that the agreement between the estimated and observed numbers is close:

		Difference.
For the Thigh	average of 6 cases =	+1.10%
For the Shank	average of 2 cases =	— .28%
For the Foot	average of 2 cases =	*

*The necessary observations for the foot are lacking, though the agreement would probably be close there also.

5. Some of the afferent fibers are distributed to the muscles. The proportion in the thigh is highly variable. The one case available shows a larger proportion of afferent fibers to the muscles of the shank than to those of the thigh, suggesting that in the foot the proportion would be still greater.

Thus, while the number of afferent fibers in a segment appears to be in proportion to the area of the skin, yet the distribution of these fibers is both to the skin and the muscles. The significance of this arrangement can only be determined by work on other forms, both higher and lower than the frog, in the zoölogical scale.

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THE RATE OF THE NERVOUS IMPULSE IN THE VENTRAL NERVE-CORD OF CERTAIN WORMS.

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(From the Hopkins' Seaside Laboratory and the Physiological Laboratory of Leland Stanford, Jr. University.)

With 14 Figures.

The physiological properties of the muscles in different species of worms have been investigated by BIEDERMAN (**1**, 1889), FÜRST (**2**, 1889), UEXKÜLL (**3**, 1896), BOTTAZZI (**4**, 1898), STRAUB (**5**, 1900), and BUDDINGTON (**6**, 1902), and the physiological effects of sectioning the ventral nerve cord, extirpation of portions of the same, and extirpation of the œsophageal ganglia have been studied by LOEB (**7**, 1894), FRIEDLÄNDER (**8**, 1894), and MAXWELL (**9**, 1897); but no observations on the rate of propagation of the nervous impulse appear to have been made in this phylum. In this paper we record some measurements, done by the graphic method, of the rate of nervous impulse in the following species:

Cerebratulus sp.[1]	Sthenelais fusca Johnson
Aulastomum lacustre	Eunice sp.
Cirratulus sp.[2]	Nereis virens Sars = N. branti Ehlers
Arenicola sp.	Nereis sp.
Bispira polymorpha Johnson	Lumbriconereis sp. (a)
Aphrodite sp.	Lumbriconereis sp. (b)
Polynoe pulchra Johnson	Glycera rugosa Johnson

[1] The two nemertians worked on were identified for us by Professor R. W. COE of Yale University as belonging to this genus, species probably new.

[2] The marine annelids were identified for us by Professor H. P. JOHNSON of Harvard University. Some of them are new species described by Professor

The work on the marine forms was done at the Hopkins' Seaside Laboratory, Pacific Grove.

A simple muscle-nerve preparation suitable to the graphic method is not obtainable in the worms. The preparation we employed consisted of the ventral nerve-cord in connection with an anterior or a posterior part of the worm serving as a reacting portion. This may be called a muscle-nerve-cord preparation to distinguish it from the simple muscle-nerve preparation. The length of the nerve-cord obtainable for this preparation is considerable in some members of the group, and the muscle part, especially if prepared from the anterior end of the animal, is strong enough to raise a light lever. The extreme posterior end of the worm can be used for a reacting portion in few forms only, owing to its greater fragility. The length of the reacting portion can be suited to any case; we found a length that gave a height of contraction of 10 to 20 mm. as magnified by the lever most convenient, but in worms with well developed chitenoid epidermis a less height of contraction had to suffice.

The apparatus used in the present work was much the same as that used by us in the work on the determination of the rate of impulse in molluscs (**17**, 1903). Many difficulties were encountered in preparing the worms for experimentation, but after many unsuccessful attempts the following method was found most serviceable. The animal was securely fixed by dissecting needles, ventral side down, to the moveable floor of a large moist chamber supported on a universal stand, the point of fixation being sufficiently posterior or anterior to give the desired length of the reacting portion. In case it was desired to prepare the reacting portion from the anterior part of the animal the extreme posterior end was then secured in the same manner, care being taken that the anterior and posterior points of fixation were so close together that maximal longitudinal contraction of the worm between these two points exerted lit-

JOHNSON (Preliminary Account of the Pacific Coast Annelids, *Proc. Cal. Acad. Sci.*, 3rd ser. Vol. I, No. 5, 1897; the Polychaeta of the Puget Sound Region, *Proc. Bost. Soc. Nat. Hist.*, Vol. 29, No. 18, 1901); and the species not named are now in his hands for study.

tle or no pull on the needles, for when this is the case the worm breaks in two. The body of the worm was secured to the board as before in two places: one about 1 to 2 cm. anterior to the last and the other about the same distance posterior to the first point of fixation, care being taken in all cases not to injure the nerve cord. Between the two anterior and posterior fixed points the body of the animal was laid open by a longitudinal dorso-median incision through the body wall. The body wall was pinned out to either side and the exposed viscera were turned to one side or removed. The nerve cord was dissected free from the adjacent tissue and the entire musculature completely severed near the reacting portion, so that this was in connection with the rest of the body by the nerve cord only. The freed portions of the nerve cord were placed on the distal and the proximal pair of platinum electrodes respectively, and the muscle was connected with the lever by means of a hook and thread passing over a friction wheel at the end of the platform. This general account applies more especially to forms like the Glyceridæ and the Lumbriconereidæ, but numerous devices such as narcotics, decapitation, etc., had to be resorted to to meet the exigencies in other groups. Variations from the general method are noted with each group.

The complete freeing of the nerve cord from adjacent tissues without impairing its function is extremely difficult, if not practically impossible, in most worms, partly because of the small calibre of the cord, and partly because of its more or less complete investment by the ventral musculature. In Nereis virens the nerve cord is large and therefore comparatively easily freed; in Aulastomum, Aphrodite and, to some extent, in Arenicola, the cord runs free in the body cavity; but with these exceptions we never succeeded in completely freeing the cord from the ventral musculature.

The severing of the dorso-lateral musculature (the ventral musculature is severed by the dissecting out of the nerve cord) between the two points of fixation nearest the reacting portion was done to prevent complications by possible myelo-conduction. At the time, we were not acquainted with FRIEDLÄNDER'S obser-

vation (**8**, 1894) on Lumbricus that the contraction of the worm on stimulating any part of the body does not extend beyond the segment where the ventral nerve cord has been severed. But this severing of the musculature involves considerable injury, especially to worms like the Sabellidæ and Aphroditæ, and to avoid this we ascertained by severing the nerve cord and stimulating the worms anterior and posterior to the cut that the contraction with which we had to do in our experiments never passes beyond the segment where the cord is cut, either in the postero-anterior or the antero-posterior direction. This fact makes the operation unnecessary, and it was therefore dispensed with in the subsequent work.

Owing to the necessity of having the fixation points, that is, the points of application of the two pairs of electrodes, close enough together to prevent the preparation from breaking off when being stimulated, the actual distance between the electrodes could not be taken as a measure of the distance of nerve cord traversed by the impulse. At the end of the experimentation the segments were counted and the distance measured, or more properly estimated, the preparation being stretched as nearly as possible like the normally crawling worm or after it was killed in fresh water. The last method has this advantage that it gives uniform results but it may not approximate the true distance any closer. It goes without saying that neither method gives accuracy. This is especially true of forms with only slightly developed chitenoid epidermis like the Sabellidæ and Glyceridæ and therefore capable of great elongation and contraction. In the Nereidæ the distance can be measured more accurately. In Aphrodite and Aulastomum the entire length of the cord was dissected out and measured. In addition to this difficulty of obtaining accurate measurements of the nerve cord other difficulties and serious sources of error were encountered in the experimentation, chief among these the activity or "spontaneous" contractions of the reacting portion and its unequal degree of relaxation at the moment the records were obtained, and the fact that the same strength of stimulus usually caused greater contraction when applied by the prox-

imal electrodes to the nerve cord near the reacting musculature than when applied by the distal electrodes some centimeters away from the reacting portion. The incessant relaxation and contraction caused, no doubt, in part by the injury in the dissection and by the pull of the lever, are almost entirely absent in forms like Bispira and Cirratulus; they are quite pronounced in Glycera and Lumbriconereis and even more so in Aulastomum, while in Lumbricus they present difficulties which we have thus far been unable to surmount. The unequal relaxation of the musculature at the moment of stimulation caused variations in the height of contraction, which, together with the unequal efficiency of the distal and proximal stimuli, rendered comparison of the tracings very difficult, as little guidance could be had in the height of contraction. We found, however, that in many instances the height of contraction varied 50% without any appreciable variation of the latent time. But the latent time seemed to vary with the strength of the stimulus, and stronger stimuli were always used for the stimulation by the distal electrodes to secure approximately the same height of contraction as on proximal stimulation. The electrodes nearest the reacting musculature were always placed one to four centimeters from it and additional precautions were taken to insure against direct stimulation of the muscle by escape currents.

The measurements are tabulated in summaries for each species, but to give an idea of the make-up of these summaries the standard deviation and the coefficient of variability of individual measurements of one typical experiment are given. The figures present a representative pair of records from each species. The relaxation phase of the myograms is much prolonged and in many cases very irregular, but as this does not directly concern the present work only the part of the tracings showing the latent time and the height of contraction is given.

Most of the experiments on the marine forms were carried out during the summer of 1901 and 1902, but some records were also obtained during the winter seasons. In the winter the temperature of the aquarium varied from 11°C. to 20°C.,

in the summer from 12°C. to 14°C. The temperature recorded in the case of Aulastomum is that of the room.

Cerebratulus sp.

Several species of Nemertians are found in abundance at Pacific Grove, but most of them are of too delicate a structure to be experimented with by the method employed by us.

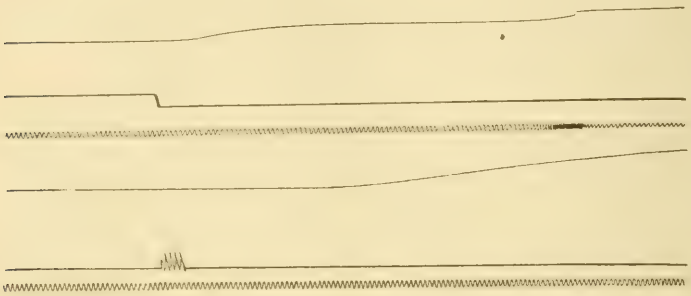


Fig. 1. Cerebratulus sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 5 cm. Rate: 8 cm. per sec. Time: 50 d. v. per sec.

We succeeded in securing but two specimens of Cerebratulus of sufficient strength. These specimens were about 30 cm. in length, but showed the same tendency to break into small fragments on irritation, that was manifested by their smaller relatives. Decapitation failed to quiet them. However, we secured an unbroken portion of a few centimeters in length from the anterior part of each specimen. The Nemertians possess one dorsal and two lateral longitudinal nerve cords, in which they resemble the Platodes rather than the Annelids. No attempt was made to isolate the nerve cords. The stimulus reached the cord by application of the electrodes to the ventral side of the body. Single induction shocks were not always sufficient for excitation from the distal point of stimulation. The required intensity of the stimulus is much greater in this species than in any of the Annelids included in this work.

The length of the portion of the nerve cord between the two points of stimulation was determined in the specimen while crawling in the aquarium.

EXPERIMENT NO. 1, Table I, Dec. 26, 1901.

	Distal	Proximal
No. of records	6	6
Mean latent time	1.76 sec.	0.29 sec.
Standard deviation	0.174 sec.	0.06 sec.
Coefficient of variability	.10	.20

Length of cord : 8 cm. Rate : 5.44 cm. per sec.

TABLE I.

Summary of experiments on *Cerebratulus sp.* Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	6	6	8	5.44
2	5	5	5	9.0

Aulastomum lacustre.

(*Horse Leech.*)

Through the kindness of Mr. J. C. BROWN of the Department of Animal Biology of the University of Minnesota, we received a number of large individuals of this species from Lake Vermillon, Minn. They thrived well in the aquarium, some

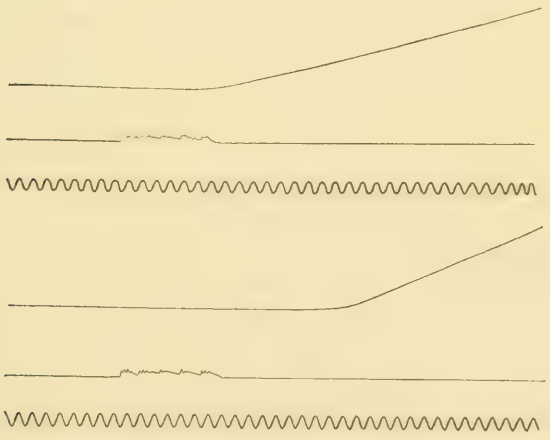


Fig. 2. Aulastomum lacustre. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 11 cm. Rate: 63.8 cm. per sec. Time : 50 d.v. per sec.

being kept for over three months. The preparations used may be therefore regarded as from individuals in good condition.

The muscle-nerve-cord preparation was made as in the other members of this series. It was found after experimenting with one specimen that the dissection of the cord for its whole length produced too great injury to it, and such extended dissection is unnecessary. The cord is fairly free and easily accessible to the electrodes. No precaution against its breaking itself in pieces is necessary with the leech. Unfortunately, the dissection necessary to make the preparation caused the posterior portion of the animal to contract so strongly that it would not react to further stimulus and hence could not be used to make records of contractions. Consequently we were unable to determine the antero-posterior rate in the cord. The head end, however, being free from this prolonged contraction allowed the determination of the postero-anterior rate. This was not without difficulties, for the almost incessant motion of the anterior part of the animal, thus continually displacing the lever attached to it, makes it necessary to watch very closely to catch the moment of rest of the animal, coinciding with proper adjustment of apparatus. Still, when all was right, the stimulus gave prompt and decisive reaction. These conditions made it obviously impossible to take the records at equal intervals.

It was found necessary to make use of the interrupted current, for, while single induction shocks were efficient as a stimulus when applied at the point of the cord nearest the musculature used, they failed to produce a definite contraction when applied at the distal point. This was true for both directions in the cord. However, a single induced shock applied to a point in the posterior end of the cord generally produced the indefinite motion of swimming or crawling.

At the conclusion of each experiment the worm was killed in 5% alcohol, the cord dissected out, and measured after taking the precaution to straighten out the loops formed in the interganglionic portions produced by the contraction of the body of the leech.

The temperature of the room varied from 16°C. to 21°C.

EXPERIMENT No. 2, Table II, Oct. 5, 1901.

	Distal	Proximal
No. of records	23	23
Mean latent time	0.28 sec.	0.11 sec.
Standard deviation	0.03 sec.	0.004 sec.
Coefficient of variability	.10	.036

Length of cord: 10.25 cm. Rate: 59.4 cm. per sec.

TABLE II.

Summary of experiments on *Aulastomum lacustre.*
Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	14	17	10.50	42.0
2	23	23	10.25	59.4
3	7	4	10.50	39.9
4	28	27	10.50	57.7
5	15	18	10.25	48.2
6	8	9	10.50	45.1
7	29	25	11.00	47.0
8	18	21	10.50	87.1
9	11	15	11.00	57 2
10	12	6	10.50	80.8
11	26	16	11.00	91.3
12	16	19	11.00	37.5
13	18	26	10.50	52.5

Mean rate: 56 cm. per sec.
Standard deviation: 16.
Coefficient of variability: .28.

Cirratulus sp.

This species is very common at Pacific Grove where it is found under the rocks and in their crevices throughout the littoral zone. It reaches a length of fifteen to twenty cm. The posterior portion of the body is very slender and fragile and too

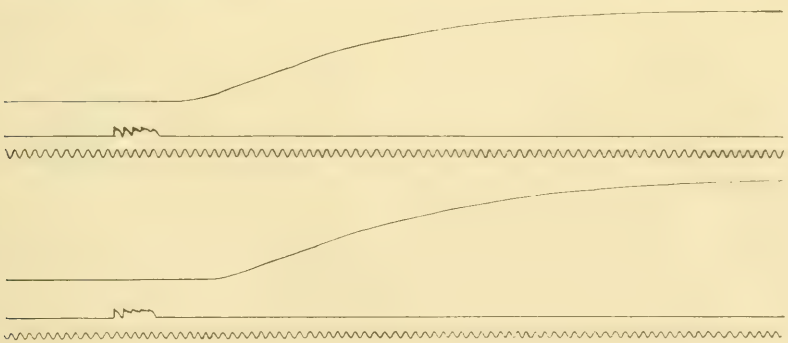


Fig. 3. Cirratulus sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 9 cm. Rate: 100 cm. per sec. Time: 50 d.v. per sec.

feeble to raise the lever of the apparatus, consequently the antero-posterior rate was not determined. The head end, how-

ever, reacts well to stimuli to different points in the cord and allows the determination of a postero-anterior rate. On first making the preparation the head end contracts strongly, but in a few minutes it relaxes, and afterwards the preparation is fairly quiet, reacting only to the stimulus from the electrodes. A single induced shock applied to a point in the posterior portion of the cord usually produced contractions in its immediate vicinity which extended a short distance only, not reaching the head. However, a weak interrupted current of short duration produced a contraction which reached the anterior end.

The preparations fatigue quickly, so that only a few comparable tracings can be obtained in each case.

The length of the nerve cord was measured in the preparations after being killed in fresh water.

EXPERIMENT No. 4, Table III, postero-anterior, Aug. 16, 1901.

	Distal	Proximal
No. of records	3	3
Mean latent time	0.28 sec.	0.17 sec
Standard deviation	0.009 sec.	0.01 sec.
Coefficient of variability	.03	.05

Length of cord 10 cm. (105 segments). Rate: 90.9 cm. per sec.

TABLE III.

Summary of experiments on *Cirratulus sp.*

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	3	3	13	85.8
2	6	8	15	82.5
3	4	4	18	86.4
4	3	3	10	90.9
5	2	5	9	99.9
6	4	4	9.5	86.4

Mean rate: 90 cm. per sec.
Standard deviation: 1.66.
Coefficient of variability: .013.

Arenicola sp.

This worm as judged by the number of its egg masses seen during the breeding season is common in the vicinity of Pacific Grove. However, the sand in which it lives is so filled with large rocks that it is difficult to collect it. Only three workable specimens were obtained. It is very sluggish in its move-

ments. In attempting to make the nerve-cord-muscle preparation the musculature is thrown into strong and prolonged contraction. That of the circular musculature was the most marked especially at the points where the worm was fastened to the floor of the apparatus. This contraction of the circular musculature was so vigorous as to prevent the longitudinal musculature from shortening the body and thus acting on the lever. A

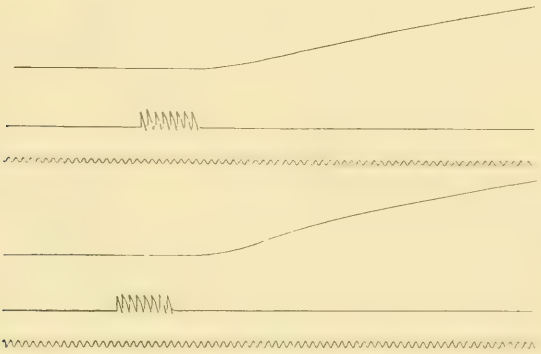


Fig. 4. Arenicola sp. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 10 cm. Rate: 125 cm. per sec. Time: 50 d.v. per sec.

dorsal longitudinal slit throughout the preparation did not lessen the effect of the circular contraction, but put the preparation in such a condition that the contraction of the longitudinal layer on stimulation of the cord bent the preparation to the inner side and in this way gave opportunity to attach the recording lever. The nerve cord is about 0.7 mm. in diameter and easily separated from the adjoining tissue. The interrupted current was used, since single induction shocks proved inefficient.

EXPERIMENT No. 3, Table IV, antero-posterior, temp. 14.5°C, July 9, 1902.

	Distal	Proximal
No. of records	12	7
Mean latent time	0.20 sec.	0.12 sec.
Standard deviation	0.01 sec.	0.007 sec.
Coefficient of variability	.05	.06

Length of cord: 10 cm. Rate: 126 cm. per sec.

TABLE IV.

Summary of experiments on *Arenicola sp.*

Antero-posterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	26	14	9	128.7
2	41	30	15	106.5
3	12	7	10	126.0

Mean rate: 120.6 cm. per sec.
Standard deviation: 9.
Coefficient of variability: .07.

Bispira polymorpha.

This large tube inhabiting worm is very abundant near the lower limits of the tides. Their tubes are so well hidden in the crevices of the rocks and so firmly attached to them, that it is only with difficulty and great care that they can be removed without injury to the occupants. When undisturbed the head

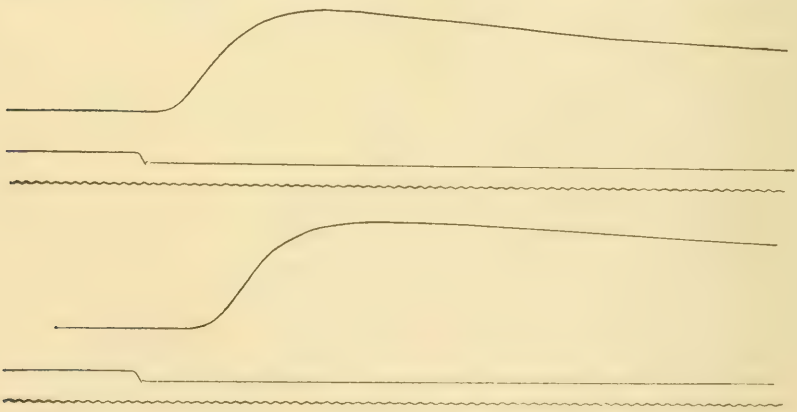


Fig. 5. Bispira polymorpha. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 28 cm. Rate: 700 cm. per sec. Time: 100 d.v. per sec.

of the worm with the mass of constantly moving tentacles is protruded from the tube. On being disturbed it suddenly retracts its head and tentacles into the tube. Conformably with its mode of life, the musculature of the anterior portion of the body is greatly developed, especially that of the longitudinal

layer, while that of the posterior portion is comparatively little developed and is feeble in its action. On the other hand, the contraction of the anterior portion was quick and powerful, readily lifting a weight of 1000 grams. Consequently while the preparations allowed the determination of the postero-anterior rate in the cord, the antero-posterior rate was not obtained.

On account of the difficulties in dissecting out the cord and the chances of injury to it on approaching it through the dorsal side, the nerve-cord preparation in this worm could not be made in the same way as was done in the other worms. It was treated as follows: The worm was pinned to the board dorsal side down; a longitudinal incision was made through the body wall on each side about one mm. from the median line on the ventral side; this ventral strip was further freed from all connection with the organs in the body cavity. This strip containing the uninjured ventral cord was raised and placed on the electrodes. While this method, used with care, kept the cord uninjured, it presented the apparent disadvantage of placing a comparatively large thickness of tissue between the cords and the electrodes. This did not, however, prove of any disadvantage, as vigorous responses were obtained from single break induction shocks even on stimulation at the posterior point, when the secondary coil was 24 cm. from the primary. The anterior 12 to 15 segments were used as the reacting portion, leaving from 17 to 20 cm. of nerve-cord between the points of stimulation. The lever was weighted with from 20 to 25 grams. A single break induction shock produces a single prolonged contraction. The preparation is not easily fatigued. Anaesthetics were found not to be necessary. The length of the nerve used was measured after the preparation was killed in fresh water. Their length, thus killed, corresponds to that of the animals undisturbed in the aquarium but freed from their tubes. In this condition the worm is from 12 to 15 cm. shorter than than in its tube.

EXPERIMENT No. 10, Table V, postero-anterior, temp. 14°C, Jan. 2, 1902.

	Distal	Proximal
No. of records	11	7
Mean latent time	0.057 sec.	0.024 sec.
Standard deviation	0.0022 sec.	0.002 sec.
Coefficient of variability	.04	.08

Length of cord: 20 cm. (150 segments). Rate: 606 cm. per sec.

TABLE V.

Summary of experiments on *Bispira polymorpha*.

Postero-anterior rate.

No of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	12	12	18	691
2	2	2	15	555
3	2	2	18	817
4	15	16	20	952
5	16	15	19	729
6	11	11	17	629
7	8	8	20	714
8	4	2	20	526
9	6	4	17	680
10	11	7	20	606

Mean rate: 694 cm. per sec.
Standard deviation: 93.
Coefficient of variability: .13.

Aphrodite sp.

An undetermined species, probably new, of this interesting Polychæte occurs in the vicinity of Pacific Grove. As it lives in rather deep water and seems not to be common it is only occasionally brought in by the fishermen. We have secured thus

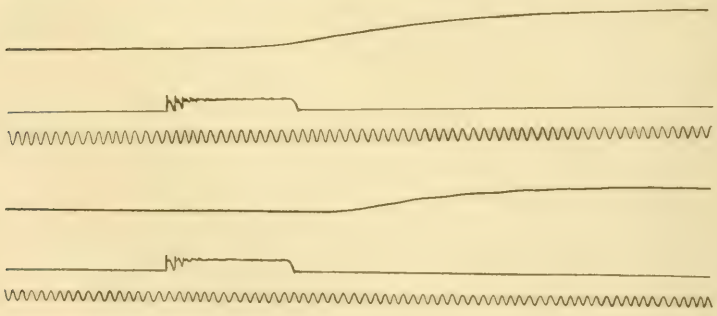


Fig. 6. Aphrodite sp. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 8 cm. Rate: 52.8 cm. per sec. Time: 50 d.v. per sec.

far but two uninjured specimens, the largest of which measured 12 cm. in length and 5 cm. in breadth. This worm is very slow in its movements and it was found to possess a rather low irritability since single induction shocks failed to procure a reaction when applied to the distal point of stimulation. The

complicated dorsal structures of this worm together with the powerful contractions on irritation contribute to render the making of nerve-cord-muscle preparations difficult. The red pigmented nerve cord is nearly free in the body cavity and when the body is contracted the cord is thrown into loops, which necessitated the taking the cord out and straightening it before measuring the length involved. The musculature of the posterior end was taken as the reacting portion, and the antero-posterior rate only was determined. Although single induction shocks were not efficient at the distal points of stimulation to produce contractions in the longitudinal muscles of the reacting portion, they were found to be sufficient to set up a progressive movement of the setæ from the point of stimulation posteriorly, indicating that their neuro-muscular apparatus is more irritable. This seemed to be further indicated by the fact that the animal could be quite roughly handled without producing contractions of the longitudinal muscles, while the setæ reacted to the treatment.

EXPERIMENT No. 2, Table VI, antero-posterior, temp. 15°C, Jan. 19, 1902.

	Distal	Proximal
No. of records	25	18
Mean latent time	0.422 sec.	0.26 sec.
Standard deviation	0.045 sec.	0.03 sec.
Coefficient of variability	.10	.11

Length of cord: 9 cm. (17 segments). Rate: 56.25 cm. per sec.

TABLE VI.

Summary of Experiments on *Aphrodite sp.*

Antero-posterior rate.

No of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	34	31	8	52.8
2	26	18	9	56.25

Average rate: 54.5 cm. per sec.

Polynoe pulchra.

This worm lives on the surface of the oral tentacles of the large sea cucumber, *Holothuria californica*, and in the mouth cavity of the large key-hole limpet, *Lucopina crenulata*, both of which are common at Pacific Grove. This species of Polynoe reaches a length of from 4 to 5 cm. On account of the delicacy of its structure the nerve-cord is exposed with some difficulty. The worm also breaks in pieces very readily, neither chloralhy-

drate nor decapitation serving to quiet it. These obstacles prevented our obtaining satisfactory records from more than two specimens, although many specimens were attempted. The preparation fatigues quickly and single induction shocks, unless very strong, were not always efficient. Only the postero-anterior rate was determined. Another species of this genus, Polynoe brevis, is common at Pacific Grove, but as it reaches a length of only 2 or 3 cm. no records could be taken from it.

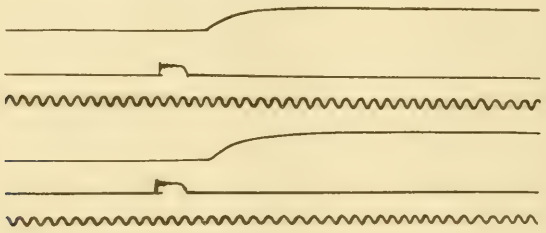


Fig. 7. Polynoe pulchra. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 3.5 cm. Rate: 350 cm. per sec. Time: 50 d.v. per sec.

EXPERIMENT No. 1, Table VII, postero-anterior, temp. 13°C, Aug. 16, 1901.

	Distal	Proximal
No. of records	2	2
Mean latent time	0.127 sec.	0.110 sec.
Standard deviation	0.004 sec.	none
Coefficient of variability	.03	none

Length of cord: 4 cm. (33 segments). Rate: 230 cm. per sec.

TABLE VII.

Summary of experiments on *Polynoe pulchra.*

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	2	2	4	236
2	2	2	3.5	350

Average rate: 293 cm. per sec.

Sthenelais fusca.

This worm seems to be rare at Pacific Grove. Satisfactory records for a single specimen only were obtained, and these are of the rate of the impulse in the postero-anterior direction.

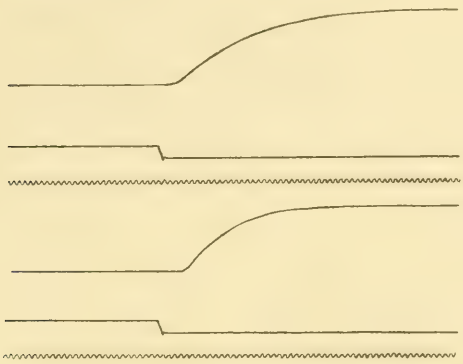


Fig. 8. Sthenelais fusca. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 5 cm. Rate: 250 cm. per sec. Time: 100 d.v. per sec.

TABLE VIII.

Detail of experiment on *Sthenelais fusca.* Dec. 31, 1902.

Postero-anterior.

	Total latent time in sec.	
	Distal	Proximal
	.065	.025
	.045	.028
	.055	.028
	.050	.029
	.045	.028
	.048	.025
Average:	.051	.027

Transmission time: 0.024 sec.
Length of cord: 5 cm. (53 segments).
Rate: 205 cm. per sec.

Eunice sp.

This worm, fairly abundant, lives under rocks in tubular passages formed by cementing particles of gravel together. It attains a considerable length, specimens 25 cm. long being taken. It breaks into pieces very readily. For this reason, and further, because of its violent struggling in being captured, an unbroken specimen was rarely secured.

When being prepared for experimentation in the usual manner, Eunice always broke in pieces unless it was previously

decapitated, but even the decapitated preparation would sometimes twist itself in two. Chlorhydrate had the same quieting effect as decapitation.

Eunice is very quick in its movements and compares in irritability with Polynoe and Nereis. Single induced shocks were efficient stimuli, the reacting portion responding generally with a single prolonged contraction.

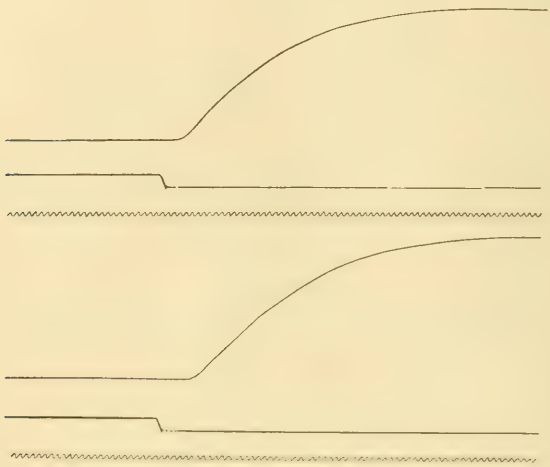


Fig. 9. Eunice sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 9 cm. Rate: 450 cm. per sec. Time: 100 d.v. per sec.

The measurements were made after the preparation had been killed in fresh water, which gives nearly the same extension as when the worm is lying quiet in the aquarium.

The antero-posterior rate alone was determined.

EXPERIMENT No. 3, Table IX, postero-anterior, Dec. 26, 1902.

	Distal	Proximal
No. of records	13	12
Mean latent time	0.050 sec.	0.038 sec.
Standard deviation	0.003 sec.	0 0023 sec.
Coefficient of variability	.060	.061

Length of cord: 5.7 cm. Rate: 474.8 cm. per sec.

TABLE IX.

Summary of experiments on *Eunice sp.*

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	2	2	9	473.4
2	3	3	4.5	409.0
3	14	12	5.7	474.8
4	13	12	13.0	520.0

Mean rate: 466 cm. per sec.
Standard deviation: 41.
Coefficient of variability: .09.

Nereis sp.

This species is very common at this point. It is found under rocks and crevices, attaining a length of 15 cm. The posterior third of the body is too weak and fragile to raise the lever, hence the antero-posterior rate was not determined. Unless it was first decapitated the conditions of the experiment invariably threw the worm into violent contractions by which it broke into pieces. The activity and irritability of this worm

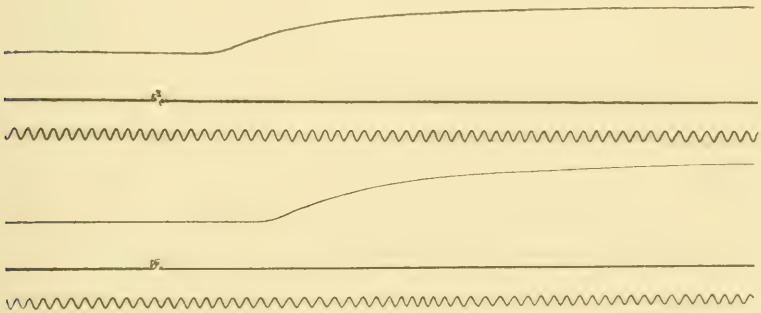


Fig. 10. Nereis sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 12 cm. Rate: 133.2 cm. per sec. Time: 50 d.v. per sec.

is much the same as that of Eunice and Glycera. However it does not respond to single induction shocks as regularly as does Glycera. A single shock applied to the cord posteriorly produces a contraction anterior to the point of stimulation, the distance to which the contraction extends depending on the intensity of the stimulus. Still, the contraction does not always reach the head even with a high intensity of stimulus. The interrupted current is more sure of producing this effect.

The length of nerve-cord between the points of stimulation was measured after the preparation was killed in fresh water, in which the condition is very near the normal extension of the worm.

EXPERIMENT No. 2, Table X, postero-anterior, Aug. 7, 1901.

	Distal	Proximal
No. of records	8	9
Mean latent time	0.095 sec.	0.061 sec.
Standard deviation	0.003 sec.	0.0046 sec.
Coefficient of variability	.031	.075

Length of cord: 5.5 cm. (45 segments).
Rate: 165 cm. per sec.

TABLE X.

Summary of experiments on *Nereis sp.*

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	4	4	10.0	164
2	8	8	5.5	165
3	9	9	12.0	223.2
4	3	3	5.0	156.0
5	4	4	12 0	123.6

Mean rate: 165 cm. per sec.
Standard deviation: 32.
Coefficient of variability: .19.

Nereis virens Sars (=N. branti Ehlers).

This species seems to be quite rare at Pacific Grove, since but one specimen was secured during extended collecting in the summers of 1901 and 1902. The specimen was about 100 cm. in length and from 1 to 1.5 cm. in diameter, but it unfortunately broke into several pieces through its contractions when being captured and the piece containing the head, which was the largest, broke up further in attempting to submit it to the experimental conditions. Decapitation served to quiet its motions, and, no doubt, a much longer portion could have been obtained if this treatment had been used at first. The ventral cord was from 1 mm. to 1.5 mm. in diameter, which large size together with its favorable position in the body allowed it to be easily dissected free. Two pieces were used, one with the head contained 85 segments and gave an available distance of cord of 20 cm. The other was from near the tail and contained 25 segments with 6.5 cm. of cord available. These dis-

tances were measured while the pieces were crawling in the aquarium and represent very nearly the length during the natural extension of the worm.

Single induction shocks applied to the distal point of stimulation produced a single prolonged contraction. After three or four reactions, single shocks failed at the distal point, then the break or make of the direct current was still efficient. Since the largest preparation was no more than one-fourth the length of the whole worm, it is impossible to say whether through the whole length of the cord a single induction shock would prove efficient.

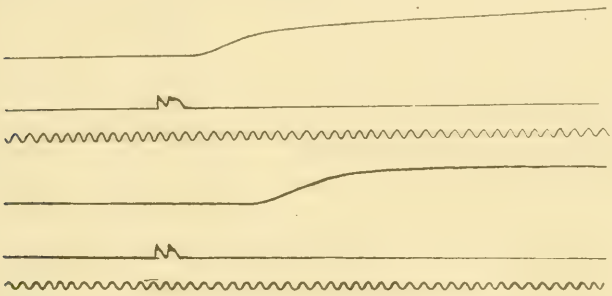


Fig. 11. Nereis virens. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 6.5 cm. Rate: 81.2 cm. per sec. Time: 56 d.v. per sec.

Good reactions were obtained from one portion 24 hours after its separation from the rest of the body; in other pieces 48 hours later only feeble responses were obtained; however one piece lived three weeks in the aquarium, when it was destroyed by an accident. In one piece the rate was taken in the antero-posterior direction, in the other postero-anterior direction. The rates 89 and 73.4 respectively, differing as they do, may not be taken, in the absence of other experiments, as conclusive evidence that the rates in the two directions differ.

EXPERIMENT No. 1, Table XI, antero-posterior, July 20, 1901.

	Distal	Proximal
No. of records	27	19
Mean latent time	0.183 sec.	0.096 sec.
Standard deviation	0.016 sec.	0.007 sec.
Coefficient of variability	.08	.07

Length of cord: 6.5 cm. (25 segments).
Rate: 73.4 cm. per sec.

TABLE XI.

Summary of experiments on *Nereis virens*.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1 (antero-posterior)	27	19	6.5	73.4
2 (postero-anterior)	13	11	20.0	89.0

Lumbriconereis sp. (a).

Small specimens of this species of 20 to 30 cm. and from 2 to 3 mm. in diameter are very abundant in the gravel at the lower limits of the tide, but only one large specimen was secured. This was 75 cm. in length and from 6 to 7 mm. in diameter, but the specimen was accidentally broken in two pieces in being captured. The anterior portion proved of great service since since 150 good records distributed over a period of three days were obtained from it. The posterior portion failed

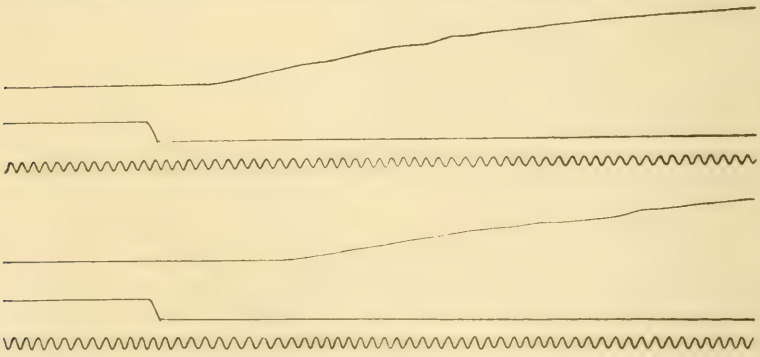


Fig. 12. Lumbriconereis sp. (a) Postero-anterior. Length of nerve cord between distal and proximal electrodes: 21 cm. Rate: 262.5 cm. per sec. Time: 50 d.v. per sec.

to give equally good results from the fact that in attempting to prepare it for experimentation it went into a strongly contracted state which continued for three days, although left undisturbed in the aquarium. During this time it failed to react to any stimuli. This same phenomenon has been observed in some of the specimens of Glycera which had been injured. The smaller specimens of Lumbriconereis gave so much trouble in this way that but few records were obtained from them. These are the only free swimming polychætes in which this phenomenon was observed.

The nerve-cord-muscle preparation can more easily be made from Lumbriconereis than from Glycera on account of its squirming less. Like Glycera, it is less easily broken than the rest of the series worked with. It is less active than Glycera but equally irritable; single induction shocks applied to the cord 20 cm. from the reacting portion produce good contractions. The measurements of the cord were taken after killing the preparation in fresh water.

EXPERIMENT No. 1, Table XII, postero-anterior, July 24 to 27, 1901.

Length of cord: 21 cm. (114 segments).

July 24 3-9 p. m.	First four pairs of records, rate: 300 cm. per sec. Total No. of records (24 pairs), rate: 65 cm. per sec.
July 25 8-11 a. m.	First four pairs of records, rate: 221 cm. per sec. Total No. of records (16 pairs), rate: 65 cm. per sec.
July 25 4-6 p. m.	First three pairs of records, rate: 210 cm. per sec. Total No. of records (15 pairs), rate: 94 cm. per sec.
July 26 9 a. m.-5 p. m.	First three pairs of records, rate: 233 cm. per sec. Total No. of records (13 pairs), rate: 80 cm. per sec.
July 27 9 a. m.	First pair of records, rate: 42 cm. per sec.

The coefficient of variability of the transmission time of the fourteen pairs of records that show a rate above 200 cm. per sec. is .37.

TABLE XII.

Summary of experiments on *Lumbriconereis sp.* (a)

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	14	14	21	241
2	3	3	9	45
3	4	4	10	45

Lumbriconereis sp. (b)

This worm is very abundant in crevices and under rocks where it constructs for itself delicate tubular passages by debris and gravel cemented together. It is commonly 30 to 40 cm. in length and from 5 to 7 mm. in diameter, but owing to its great fragility generally only portions of the worm could be secured for the preparation. The worm is rather inactive, so anæsthetics were not necessary. Despite its sluggish habits it responds to single shocks almost as readily as Glycera, but the

preparation fatigues much sooner. The measurements of the cord were made on preparations killed in fresh water, with the exception of preparation No. 7, Table XIII A., which was extended during the experimentation to the length given.

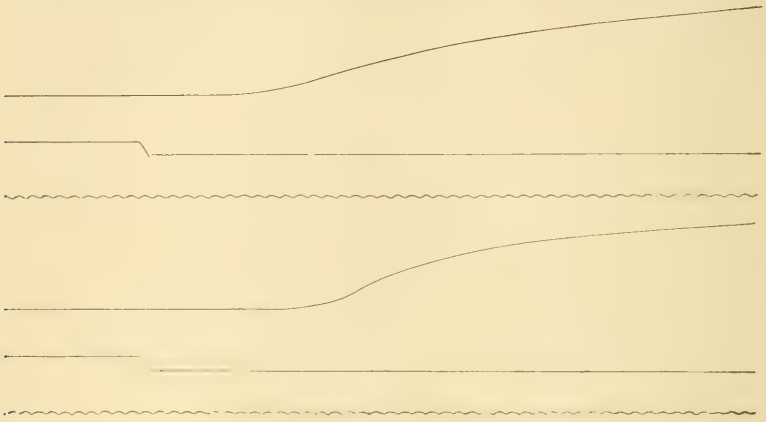


Fig. 13. Lumbriconereis sp. (b) Postero-anterior. Length of nerve cord between distal and proximal electrodes: 30 cm. Rate: 681 cm. per sec. Time: 100 d.v. per sec.

EXPERIMENT No. 4, Table XIII, postero-anterior, Aug. 7, 1902.

	Distal	Proximal
No. of records	6	6
Mean latent time	0.060 sec.	0.035 sec.
Standard deviation	0.004 sec.	0.004 sec.
Coefficient of variability	.07	.11

Length of cord: 15 cm. (125 segments). Rate: 600 cm. per sec.

TABLE XIII A.

Summary of experiments on *Lumbriconereis sp.* (b)

[redacted] Postero anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	4	2	20	40
2	5	3	13	
3	3	3	16	
4	6	6	15	
5	4	4	12	52
6	5	5	15	937
7	9	8	30	76 8

TABLE XIII B.

Summary of experiments on *Lumbriconereis sp.* (b)

Antero-posterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Dista	Proximal		
1	2	2	25	80
2	3	3	8	160
3	3	2	10	42

Glycera rugosa Johnson.

This worm is fairly abundant in the sands of the lower tide limits at Pacific Grove. The largest specimen that we collected measured from 35 to 40 cm. in length and about 13 mm. in diameter, when killed in fresh water. It is very ferocious, even in the aquaria preying on Eunice and Nereis. It is also very active,

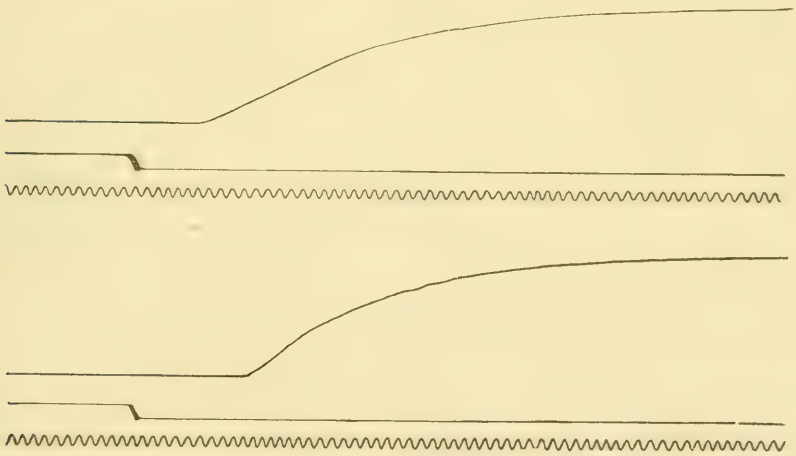


Fig. 14. Glycera rugosa. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 30 cm. Rate: 441 cm. per sec. Time: 50 d.v. per sec.

making its way through the wet sand with great speed or gliding through the water by the graceful twistings of its whole body. This worm was selected for a beginning in this work because of its large size, high irritability and strength. Glycera is less fragile than any of other free swimming polychætes worked excepting Lumbriconereis sp. (a) which equals it in this respect.

In most cases an anaesthetic, chlorhydrate, was necessary to quiet the violent squirming in making the preparation. Decapitation did not quiet these motions. The preparations responded with great regularity to single induction shocks of moderate intensity applied to the cord 20 to 30 cm. from the contracting portion; when the single shock became inefficient the interrupted current of short duration was used. The nerve-cord-preparation of this species is not easily fatigued and consequently allows a great number of records to be taken from each specimen. The preparation from one specimen, No. 2, Table XIV A, gave good responses 23 hours after it was made.

It frequently happened that an injury to any part of the body caused the musculature, both circular and longitudinal, to go into a strongly contracted state, in the immediate region of the injury. This condition in some cases continued for 24 hours, or even more, during which time it is practically impossible to send an impulse through the cord of the contracted portion. In the only case in which an impulse passed through so small a distance as 100 segments of the worm a strong interrupted current was necessary. Even in this case the responding contractions were feeble and very much delayed.

EXPERIMENT No. 2, Table XIV A, postero-anterior, July 16, 1901.

	Distal	Proximal
No. of records	32	32
Mean latent time	0.18 sec.	0.10 sec.
Standard deviation	0.014 sec.	0.003 sec.
Coefficient of variability	.08	.03

Length of cord: 34 cm. (150 segments). Rate: 425 cm. per sec.

TABLE XIV A.

Summary of experiments on *Glycera rugosa*.

Antero-posterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	21	22	34	680
2	33	32	34	425
3	11	11	25	357
4	22	22	20	400
5	4	4	25	500
6	25	25	17	425
7	11	11	20	400
8	12	11	30	375
9	9	9	24	271

Mean rate: 433 cm. per sec.

Standard deviation: 87.

Coefficient of variability: .20.

TABLE XIV B.

Summary of experiments on *Glycera rugosa*.

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	7	7	15	420
2	2	2	18	514
3	7	7	13	540
4	3	3	18	265

Mean rate: 435 cm. per sec.
Standard deviation: 106.
Coefficient of variability: .24.

TABLE XV.

Summary of the rates in the fourteen species worked on.

Species	Direction	No. of individuals	Rate in cm.	Coefficient of vari'bility
Cerebratulus sp.	Postero-anterior	2	5.4-9.0	
Aulastomum lacustre	" "	13	56.0	.28
Cirratulus sp.	" "	6	90-0	.013
Arenicola sp.	Antero-posterior	3	120.6	.07
Bispira polymorpha	Postero-anterior	10	694 0	.13
Aphrodite sp.	Antero-posterior	2	54.5	.04
Polynoe pulchra	Postero-anterior	2	293.0	.19
Sthenelais fusca	" "	1	205.0	
Eunice sp.	" "	4	466.0	.09
Nereis sp.	" "	5	165.0	.19
Nereis virens	" "	1	89.0	
" "	Antero-posterior	1	73.4	
Lubriconereis sp. (a)	Postero anterior	3	45-241	
" " (b)	" "	7	49-937	
" " (b)	Antero-posterior	3	42-160	
Glycera rugosa	" "	9	433.0	.20
" "	Postero-anterior	4	435.0	.24

In Aulastomum (table II, page 267), Cirratulus (table III, page 268), Bispira (table V, page 272), Eunice (table IX, page 277), Nereis sp. (table X, page 278), and Glycera (table XIV, page 284), the number of individals worked and the relative constancy of the individual rates seem to allow the conclusion that the mean of the individual rates is representative for their respective species. The mean in the groups represented by by two or three individuals only is of less value, especially in the two species of Lumbriconereis (tables XII and XIII) where the individual variations are so great. But in some species

thus scantily represented the individual rates show only slight variation, as in Arenicola (table IV, page 270), Aphrodite (table VI, page 273), Polynoe and Sthenelais (tables VII and VIII, pages 274 and 275), and Nereis virens (table XI, page 280), and their representative means may therefore not be far from the true rate in these species.

The rate of the nervous impulse in this series of worms is as varied as the structure and the habit of the worms themselves, the lowest being in Cerebratulus with a rate of only 5 to 9 centimeters per second and the highest in Bispira with a rate of 7 meters per second. But there seem also to be differences in rate between species in which little difference in structure and habits exists, as in the cases of Eunice and Nereis (tables IX, X and XI), the former showing a rate of 466 cm. per second, the latter a rate of 165 cm. per second.

In the species which permitted of determining the rate of the impulse in both directions of the cord (Nereis, table XI; Lumbriconereis, table XIII, and Glycera, table XIV) there seems to be no constant difference between the antero-posterior and the postero-anterior rates.

A question of considerable interest is whether the rate in the ventral nerve cord as determined in the present work represents the rate through continuous nerve fibers as in a vertebrate muscle-nerve preparation or whether the nervous paths are more complex. Our knowledge of the structure of the ventral nerve cord of the worms has been greatly advanced within the last few years through the researches of RETZIUS (**10**, 1891, 1892, 1894, 1898, 1900), RHODE (**11**, 1891), BIEDERMANN (**12**, 1891), LENHOSSÉK (**13**, 1892), FREIDLÄNDER (**14**, 1894), APÁTHY (**15**, 1897) and HAVET (**16**, 1899). But while many of the histological elements have thus been worked out and found to be markedly uniform throughout the phylum, it seems that the number of segments with which a motor neuron comes in direct relation and the extent and relation of the small sensory fibers in the longitudinal tracts and of the central or "association cells" are yet undetermined. Even the applicability of the neuron conception to the nervous system of the worms

is called in question by APÁTHY's work. On histological grounds we cannot therefore say whether the ventral nerve cord contains such a direct nervous path extending throughout its whole length.

Nor does the present work furnish anything conclusive on this point. It is true that the muscle-nerve-cord preparations of Bispira, Glycera, Eunice, Nereis and Lumbriconereis respond to a single induced shock of low intensity; and these responses on stimulating the cord 20 to 30 cm. from the muscle in Bispira and Glycera approached the uniformity of the responses of the frog's gastrocnemius on stimulation of the sciatic nerve. And such uniformity in the response to single induced shocks has not been found to obtain in the vertebrates when complex nervous mechanisms are involved. On the other hand, such great variation of the rate in the same preparation as was observed in Lumbriconereis (page 281) can not be reconciled with the physiology of simple muscle nerve preparations as it is known in vertebrates and molluscs. In Cerebratulus, Aulastomum, Cirratulus, Arenicola, and Aphrodite the muscular response to a single induced shock applied to the nerve cord subsides few centimeters in either direction from the point of stimulation. It requires a series of shocks to obtain the muscular response if the length of nerve cord involved comprises many segments; which fact suggests a complex nervous path. But while the response of the nerve cord to a single induced shock points in some species to a complex, in others to a simple nervous mechanism, the question remains yet undecided whether in the latter cases the nervous part of the muscle-nerve-cord preparation is as simple as that of an ordinary muscle-nerve preparation.

It is of some interest to know that the lowest rate in the Annelids, that of Aphrodite, or 54 cm. per sec., is higher than the rate in the pedal nerve of the slug, Ariolimax, which we found to be 40 cm. per sec., while the rate in Glycera (430 cm. per sec.), Eunice (460 cm. per sec.) and Bispira (694 cm. per sec.) is as high and even higher than the rate in the pallial nerve of the swift moving Loligo (**17**, 1903).

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NOTES ON THE TECHNIQUE OF WEIGERT'S METHOD FOR STAINING MEDULLATED NERVE-FIBERS.

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The following is not the outcome of a systematic investigation of the technique of the method of Weigert, but simply of experiments made at various times to secure the best results on material hardened as described below. Notes were often made which have been collated and the conclusions presented, not so much as invariable improvements on the regular procedure, but as suggestions for securing better results in certain cases. In the estimation of the success of a Weigert preparation, especial weight has been attached to the number of fibers revealed in the gray and the brilliancy with which they are demonstrated.

The material consisted of portions of the central nervous system, especially the cord, of the human foetus, infant and adult. This material was fixed in formalin, in potassium bichromate and formalin, or in copper bichromate. The fixation in formalin was usually accomplished by injecting into the blood vessels formalin 1 vol. + water several volumes. After removal the brain and cord were kept in formalin 1 vol. + water 9 vols. until used. Some material which yielded fine preparations had been thus kept in formalin for three years. The material fixed in potassium bichromate and formalin was usually fixed by an injection *in situ* of potassium bichromate 5%, or stronger, several vols. + formalin 1 vol. After removal, the cord and portions of brain were further hardened in potassium bichromate 5% 9 vols. + formalin 1 vol. about a week and in potassium bichromate 5% alone for ten days to 2 weeks or so. Finally, some material, the brain and cord of a 7 months

foetus, was fixed by injection *in situ* of copper bichromate 5% 1 vol. + formalin 1 vol and further hardened, after removal, in copper bichromate 3% 9 vols. + formalin 1 vol. for about a week. A method pursued with some selachian material for the study of the cranial nerves will be described below.

In order to give an idea of the various combinations of mordanting and decolorizing tried upon the above material a condensed list is given below together with the general character of the results. The staining fluid used was either WEIGERT'S alkaline haematoxylin (abbreviated in the list to "A. h.") or a neutral haematoxylin solution composed of 1 vol. of 10% solution of haematoxylin in absolute alcohol + 9 vols. of water ("N. h."). Where the kind of haematoxylin solution used is uncertain the abbreviation is "H." The word "osmic" indicates that the section was placed in osmic acid. When this was done after the removal from the haematoxylin the section was simply rinsed in water, placed in ¼% ± solution of osmic acid for ¼ to 1 minute and then rinsed again in water, previously to decolorization.

A. Celloidin sections of material (principally cord of infant and of eight months foetus) fixed and hardened in potassium bichromate + formalin as above described:

1. Copper acetate. A. h. Pal. Failure.
2. Copper acetate. A. h., H. and N. h. Osmic. Pal. Results often good, in some cases fine preparations.
3. Copper acetate. Osmic. A. h. Pal. Not very good.
4. Copper acetate. Osmic. A. h. Osmic. Pal. Fine results.
5. Copper acetate. H. Borax-ferricyanide. Not very good results—distinctly inferior to the Pal.
6. Copper acetate. H. Osmic. Borax-ferricyanide. Somewhat better than 5.
7. Copper bichromate. A. h. and N. h. Borax-ferricyanide. Not good.
8. Copper bichromate. H. Pal. Good.
9. Copper bichromate. H. Osmic. Pal. Very good. This gave the best results of any combination.
10. Copper bichromate. N. h. Iron alum. Failure.
11. Copper bichromate + osmic. A. h. Pal. Failure.

12. Copper bichromate. Potassium bichromate + osmic. H. Pal. Not good.
13. Iron alum. A. h. Iron alum. Failure.
14. Iron alum. H. Osmic. Pal. Failure.
15. Iron alum. H. Borax-ferricyanide. Failure.
16. Iron alum. Potassium bichromate + osmic. H. Pal. Failure.
17. Potassium bichromate. A. h. and N. h. Pal. Not good.
18. Potassium bichromate. A. h. Borax-ferricyanide. Not good.
19. Potassium bichromate. Iron alum. H. Borax-ferricyanide. Fair.
20. Potassium bichromate. Iron alum. H. Osmic. Pal. Good.
21. Potassium bichromate. Iron alum. H. Pal. Not good.
22. Potassium bichromate. Iron alum. H. Iron alum. Failure.
23. Potassium bichromate + chrome alum. H. Pal. Not good.
24. Potassium bichromate + chrome alum. H. Borax-ferricyanide. Failure.
25. Potassium bichromate. Copper acetate. N. h. Osmic. Pal. Fair.
26. Potassium bichromate. Copper acetate. N. h. Borax-ferricyanide. Failure.
27. Potassium bichromate + osmic. N. h. Pal. Not good.

B. Blocks of tissue, hardened like A, imbedded in celloidin, mordanted *in toto* in copper bichromate several days. The sections made were then treated as follows:

1. A. h. (at higher temperature part of time) Osmic. Pal. Fine.
2. A. h. (at higher temperature part of time.) Pal. Not very good, lacking in brilliancy.
3. A. h. (at higher temperature part of time.) Borax-ferricyanide. Failure.

C. Cord of a seven months foetus hardened in copper bichromate + formalin as above described. The celloidin sections made were treated as follows:

1. Calcium bichromate (5%, 13 days). A. h. Osmic. Pal. Fine.
2. Copper acetate. H. Pal. Not good.
3. Copper acetate. H. Osmic. Pal. Good.
4. Copper acetate. H. Borax-ferricyanide. Failure.
5. Copper bichromate. H. Borax-ferricyanide. Not good.
6. Copper bichromate. H. Osmic. Pal. Good.
7. No further mordanting. H. Osmic. Pal. Good. These

preparations were in many cases practically as good as those that were re-mordanted, there being only a slight diminution in the intensity of the stain.

D. Cerebrum of infant. Hardened in formalin as described above. Imbedded in celloidin without mordanting. Sections made were treated as follows:

1. Copper acetate 46 hours. A. h. 1½ hours. Osmic. Pal. Not good, fibers very pale.
2. Copper acetate 46 hours. A. h. 1½ hours. Borax-ferricyanide. Not good.
3. Copper bichromate 46 hours. A. h. 1½ hours. Osmic. Pal. Not good. Somewhat better than 1.
4. Copper bichromate 46 hours. A. h. 1½ hours. Borax-ferricyanide. Not good.
5. Copper bichromate 46 hours. A. h 1½ hours. Osmic. Borax-ferricyanide. Not good.
6. Copper bichromate 46 hours. A. h. 47 hours. Osmic. Pal. Better than any of preceding.
7. Copper bichromate 46 hours. A. h. 23 hours. Osmic. Pal. Like 6.
8. Copper bichromate 46 hours A. h. 23 hours. Borax-ferricyanide. Not good.

Even the best of the above were too pale, perhaps partly, but hardly principally, attributable to the youth of the brain.

E. Cord and medulla of infant 1½ months old. Hardened in formalin as above described. Pieces mordanted *in toto*, immediately after removal from formalin, in copper bichromate 3% for seven or eight days. Imbedded in STEPANOW'S clove oil celloidin.[1]

Sections were treated as follows:

1. No further mordant. A. h. 12 hours. Osmic. Pal. Good.
2. No further mordant. N. h. 16 hours. Osmic. Pal. Very good.
3. Copper bichromate 4 hours. N. h. 15 hours. Osmic. Pal. Very fine, better than 1 and 2.
4. Copper bichromate 18 hours. N. h. and A. h. 6 hours. Osmic. Pal. Slightly inferior to 3.

[1] *Zeitschrift für wiss. Mikroskopie*, Bd. XVII, H 2, 1900.

5. Copper bichromate 18 hours. N. h., kept slightly warmed, 2 to 4 hours. Osmic. Pal. Very fine, possibly somewhat better than 3.

F. Cord, medulla and basal ganglia of child 3 years and 4½ months old. Hardened in formalin as above described and preserved in formalin for about three years before being used.

(*a*) Pieces of cord mordanted in copper bichromate 3% seven days. Imbedded in clove oil celloidin. Sections treated as follows:

1. No further mordanting. H. Osmic. Pal. Good.
2. Copper bichromate. H. Osmic. Pal. Better than 1.
3. Potassium bichromate + osmic. H. Osmic. Pal. Not good.

(*b*) Pieces of cord mordanted in potassium bichromate + osmic. Sections made as in (*a*) and treated as follows:

1. No further mordanting. H. Osmic. Pal. Much better than (*a*) 3 but not nearly as good as (*a*) 1 or 2. Medullary sheaths of large fibers appear to be better fixed, however, than in (*a*).
2. Potassium bichromate + osmic. H. Osmic. Pal. Better than (*b*) 1.
3. Copper bichromate. H. Osmic. Pal. Very good, not so brilliant as (*a*) 2 but the fibers, especially in the white matter, look better than in (*a*).

(*c*) Pieces of cord mordanted seven days in potassium bichromate 5 + chrome alum 2 + water 100. Sections made as in (*a*):

1. No further mordanting. H. 12 hours. Osmic. Pal. Fair.

(*d*) Pieces of cord mordanted seven days in potassium bichromate 5%. Sections made as in (*a*).

1. No further mordanting. H. 12 hours. Osmic. Pal. Not as good as (*c*).

(*e*) Pieces of cord mordanted seven days in copper bichromate 3%. Sections made as in (*a*).

1. No further mordanting. H. 12 hours. Osmic. Pal. Fair, a little better than (*c*).

(*f*) Pieces of cord mordanted seven days in potassium bichromate + osmic. Sections made as in (*a*).

1. No further mordanting. H. 12 hours. Osmic. Pal. Fair.

(*g*) Pieces of cord mordanted seven days in iron alum 4%. Sections made as in (*a*).

1. No further mordanting. H. 12 hours. Osmic. Pal. Not good.

(*h*) Pieces of cord mordanted eight days in copper bichromate. Sections made as in (*a*).

1. No further mordanting. H. Osmic. Pal. Fair.
2. Copper bichromate several hours (kept slightly warmed). H. 22 hours (first half hour in paraffine water-bath). Osmic. Pal. Fine.
3. Potassium bichromate + osmic several hours, etc., like 2. Not good, blurred and indistinct.

[(*c*) to (*h*) inclusive, taken from some incomplete notes made by my student, C. E. DORAN].

(*i*) Pieces of medulla and basal ganglia mordanted *in toto* in copper bichromate 3% for seven or eight days. Sections made as in (*a*).

1. No further mordanting. N. h. 12 hours ± Osmic. Pal. This invariably yielded fine results with a series extending through the medulla and basal ganglia, practically as good as when remordanting in section was resorted to and without the added danger of brittleness.

The following modification of the WEIGERT method was devised by the writer in 1897 and has been found to be especially adapted for his work upon the cranial nerves of Squalus acanthias. The head of an embryo at birth, cut longitudinally vertically in two pieces so as to just open one side of the cranial cavity, was hardened for about two weeks in iron alum 5% 9 vols. + formalin 1 vol. This fluid also decalcified. Although the material was somewhat brittle, a complete series of paraffine sections was successfully made. After fixing on the slide and successive removal of the paraffine and xylol, the slides were taken from the absolute alcohol and a thin solution of celloidin poured over them and off, thus covering the sections with a thin film of celloidin and absolutely preventing their removal from the slide during subsequent manipulations. This device, which had been used by the writer for some time previously to this, very much minimizes the danger of loss in staining serial paraffine sections.

The sections were then stained, without further mordant-

ing, in the above-mentioned neutral haematoxylin for 4 to 12 hrs., the shorter period being found sufficient. As in all WEIGERT methods, old or used solutions of haematoxylin must be avoided. The sections are then decolorized in 1% or 2% iron alum, the decolorization proceeding slowly and evenly. With any degree of care, over-decolorization is easily avoided. After decolorization, the sections, now being a faint pinkish hue, are washed, dehydrated, cleared and mounted.

With this method the peripheral nerves in Squalus were well fixed and stained deep blue. The color was completely removed from all other tissues except the denticles and sometimes portions of cartilage. The central nervous system was not as well fixed nor stained, but presented a fairly good WEIGERT picture.

The decalcifying power, simplicity and certainty of this method recommend it for such work. The tendency of the iron alum-formalin to overharden and make the tissue difficult to section is perhaps the principal defect. With the loose tissues of the young shark this objection was not realized as it would be with other objects.

This method has been reported by HERRICK (*State Hospitals Bulletin* of N. Y. State, Oct., 1897, p. 27 and *Journal of Comparative Neurology*, Vol. VIII, Nos. 1–2, July, 1898.).

Conclusions. Though many of the combinations in the above lists have not been sufficiently tested, yet from these data and from other observations of the writer, the following conclusions which may in cases be of practical value may be drawn.

(*a*) Fixation and hardening in formalin alone appears to be preferable in some respects to fixation and hardening in potassium bichromate + formalin followed by further hardening in potassium bichromate. The latter method is capable of yielding fine preparations, but at times it appears difficult to secure them by the ordinary procedures. Furthermore, in such material the medullary sheaths when stained often exhibit a vacuolated appearance, due apparently to a staining of the neurokeratin network, which detracts from the brilliancy of the preparations.

It is a question whether the plain bichromate fixing and hardening be not superior in some regards.

(*b*) Formalin fixed and hardened material will apparently keep indefinitely in formalin and yet be capable of giving fine WEIGERT preparations when subjected to the appropriate treatment (*vida supra*, F). As a corollary to this it would appear advisable to keep all material to be used for WEIGERT preparations, however fixed and hardened, in formalin instead of alcohol. Material kept long in alcohol will not usually yield brilliant WEIGERT preparations.

It may be well to call attention here to the fact that sections already stained for WEIGERT but not decolorized may often be kept for months in water containing some formalin (to prevent the growth of molds etc.) and yet give good preparations when decolorized. This proved to be the case with some sections prepared as indicated above under F (*i*). There is apparently a very slight gradual loss in brilliancy. Sections stained as in F (*i*) and kept thus 1½ yrs. in 10% ± formalin still yielded good preparations when decolorized. Some of these which had been brought, after rinsing in water, into formalin and the formalin changed when discolored were practically indistinguishable, when decolorized, from those decolorized immediately after staining.

(*c*) Material fixed and hardened in formalin should in all cases be mordanted *in toto* before bringing it into alcohol preparatory to imbedding. Here lies the explanation, probably, of the discrepancy between the results obtained with formalin material by BOLTON[1] and those obtained by HERRICK.[2] BOLTON mordanted sections made from frozen or gum imbedded material, while HERRICK mordanted paraffine sections. It is also better to mordant pieces of the material immediately before they are to be used so that mordanted blocks need not be kept long before cutting and staining.

It is probable, from this, that some of the apparently bad fixation of medullated nerve fibers seen at times in formalin material is really due more to the subsequent treatment, the

[1] *Journ. Anat. Physiol.* Vol. XII, N. S., 1898. [2] *Op. cit.*

formalin fixed fibers not being so resistant as fibers impregnated with a metallic salt in the act of fixation and hardening. This view would seem to be further confirmed by the observations above noted (F (*b*)) where the fibers appeared to be in better histological condition when the formalin material was first treated with potassium bichromate + osmic than when treated in other ways. The superiority of osmic acid in faithfully fixing medullated nerve-fibers is well known.

(*d*) Preparations from pieces mordanted *in toto* can often be made more brilliant by remordanting the sections before staining. When the points noted in (*c*) have been observed, however, this may often be omitted, the gain being insignificant and the sections being liable to become brittle.

(*e*) The best mordant for WEIGERT-PAL preparations of both formalin hardened and other material is probably bichromate of copper, this apparently excelling WEIGERT'S chrome alum-bichromate mixture.

Bichromate of copper is a reagent which has some qualities to recommend it in neurological work. It was first used by the writer in 1898 and had not been previously applied in histological work as far as I am aware. It is an energetic fixing and hardening reagent, more so apparently than any other bichromate. This indicates its use, either with or without formalin, in fixing and hardening foetal brains and spinal cords and as a mordant which gives the most brilliant results when the WEIGERT-PAL method is to be used. As a hardening fluid, the results here are confined practically to the above-mentioned (*C*) cord of a 7 months foetus. The material and fibers were perhaps somewhat overhardened and shrunken but yielded very fine preparations. One hasty trial of this reagent in the method of GOLGI did not produce noteworthy results.

(*f*) Copper bichromate and other bichromates do not give good results as mordants (unless, as in the usual method, there is remordanting with copper acetate) where the borax-ferricyanide decolorizer is to be used.

(*g*) Copper acetate as a mordant invariably yields poor

results with the PAL decolorization unless osmic acid is used as indicated below (*k*).

(*h*) Iron alum did not prove to be a valuable mordant—except where used as a hardening reagent for the peripheral nerves as above described. It was still worse as a decolorizer.

(*i*) Mordanting the celloidin block *in toto* without further mordanting does not give such brilliant preparations as when the celloidin sections are mordanted instead.

(*j*) No constant differences were noted between the WEIGERT alkaline haematoxylin and the neutral haematoxylin. Certainly with the PAL decolorization the neutral is as good or possibly somewhat better.

(*k*) A slight or considerable increase in the brilliancy of WEIGERT-PAL preparations can often be obtained by dipping the sections in osmic acid for a fraction of a minute immediately after they have been removed from haematoxylin and rinsed in water. When this is done, sections mordanted in copper acetate before staining will often give good results with the PAL decolorization, though otherwise, as indicated above (*g*), they would be useless for this method.

Osmic, used in this way before the borax-ferricyanide decolorization always gave poor results.

(*l*) The time of mordanting and staining is omitted in A, B and C for purposes of condensation. When the time devoted to these processes has been too short, the stain is too pale and the finer fibers are not be well demonstrated; when too long, decolorization is too protracted and the ground will not be sufficiently decolorized or the fibers will be over-decolorized. Naturally, the longer the mordantage the shorter the time required for staining. Usually, at the temperature of the room, about 12 hrs. for mordanting and about 4 to 6 hrs. for staining were the most favorable, but no rule can be laid down, owing to the condition of the material and other factors. Heat will of course accelerate the process but this is not necessarily to be recommended, it being liable, especially when mordanting with copper bichromate, to render the sections brittle.

Dept. of Zoology,
Nov., 1903.

THE DOCTRINE OF NERVE COMPONENTS AND SOME OF ITS APPLICATIONS.[1]

By C. Judson Herrick.

The original purpose of the students of nerve components was the analysis of the peripheral nervous system into units which should have at the same time a functional and a structural significance. This obviously is not the case with the cranial and spinal nerves as commonly enumerated. The structural peculiarities of each of the twelve pairs of cranial nerves, for instance, while fairly well defined in the human body, are very diverse in the vertebrate series as a whole. Thus the facial nerve from being predominantly sensory in lower vertebrates (more than half of its fibers in fishes belonging to a sensory system not represented at all in mammals) becomes in man predominantly motor with only a vestigeal remnant of the sensory components, and even the motor component innervates chiefly muscles new to the mammalia. We might multiply illustrations of the structural instability of the cranial nerves. And that the cranial nerves have any special significance as functional units cannot be maintained for a moment, no two pairs in the human body having even approximately the same function.

But the first measurably complete analysis of the cranial nerves into their components for their entire extent showed at once the presence of certain structural and functional systems of components, the laws of whose distribution have apparently little to do with the serial order of the cranial nerves as commonly enumerated.

We have, then, a number of systems of components each of which is defined structurally by similarity of peripheral and

[1] Presidential Address delivered before the Ohio State Academy of Science, Nov. 27, 1903.

central terminal relations, and functionally by the trasmission of nervous impulses of the same type or modality. Among these systems are tactile, auditory, visual, olfactory, motor, gustatory, etc., each with very characteristic terminal relations.

Now, this structure is absolutely meaningless apart from its function. Let any one who doubts this spend a few months (as I have done) in trying to master and correlate the existing literature of the cranial nerves of vertebrates. Though these descriptions were for the most part written by famous masters of anatomical science, yet in their aggregate they present an indigestible mass of confused and meaningless detail, crude fact, well spiced with error, for the most part not worth the prodigeous labor of digging it out of the oblivion of classic tomes of by-gone anatomists.

I do not mean to imply that all the problems of cranial nerve morphology are now cleared up; but I do claim that there is no longer any necessity for the further accumulation of uncritical and meaningless fact in this field of research. We have already gone far enough to point the way toward certain lines of fruitful correlation. We can not only correlate structure with structure, but we can interpret structure by function and thus bring out a fuller meaning. We are at least coming into a realization of the fact that we cannot fully understand any structure until we know what it can do.

This point of view of course is not new, but as worked out practically in the peripheral nervous system it is exerting a clarifying influence upon our knowledge of the central system also. The present demand in cerebral anatomy is for conduction paths, for functional systems of neurones, and precise knowledge of the pathways between the brain and the periphery is the first step in such a central analysis.

The primary function of the nervous system is to facilitate the reaction of the organism to the external forces of the environment. Later, as the reacting mechanism becomes more complicated, the nervous system assumes the function of coordinating this mechanism, i. e., of reaction to the forces of the internal environment. These two functions lie at the basis of

our most fundamental division in the analysis of the nervous system; viz.: (1) the somatic systems (sensory and motor) for bodily responses to external stimuli, and (2) the visceral systems (sensory and motor) for visceral reactions to internal stimuli.

Each of these great divisions has been analyzed peripherally, more or less imperfectly as yet, into systems of components, as suggested above. Every such system of nerve fibers performs a separate function, conducts a single type of nervous impulse, either afferent, i. e., sensory, or efferent, i. e., excito-motor, excito-glandular, etc. The following systems are already distinguishable anatomically:

I. SOMATIC SYSTEMS.
 1. *Tactile*, or *general cutaneous*.
 2. *Acustico-lateral*, including nerves for lateral line organs (in the Ichthyopsida) and for organs of equilibration and hearing (in vertebrates generally). These organs and their nerves have probably been derived phylogenetically from the general cutaneous system and, like the organs of the latter type, are adapted for the reception of various kinds of mechanical impact, either rhythmic or non-rhythmic.
 3. *Visual* (a system of uncertain relationships, provisionally classified under the somatic sensory).
 4. *Somatic motor*, for the innervation of skeletal or voluntary muscles.

II. VISCERAL SYSTEMS.
 5. *Visceral sensory*, unspecialized sensory nerves of the viscera, distributed chiefly through the sympathetic nerves.
 6. *Gustatory*, innervating specialized sense organs (taste buds) of chemical sense probably derived phylogenetically from the preceding type.
 7. *Olfactory* (provisionally classified here because of the apparent resemblance between taste and smell).
 8. *Visceral motor*, distributed chiefly to unstriped and involuntary muscles, generally through the sympathetic system.
 9. *Excito-glandular*, provisionally classified here because of genera resemblance to the last mentioned type.

There are numerous other systems which can be differentiated physiologically, but which cannot as yet be completely separated anatomically and classified, such as nerves for the

thermal sensations, muscle sensations, etc., but enough has been done to enable us to lay down the general plan or pattern of the peripheral nervous system as a whole and to define the main pathways by which stimuli of different modalities reach the brain and are reflected back to the responsive organs. Our anatomical knowledge of these pathways is sufficiently well controlled by precise physiological experimentation to enable us to state with confidence that each of the nine systems mentioned above is a real functional unit.

The fibers composing these systems may reach the central nervous system through a series of many nerve roots arranged in a segmental way, like the general cutaneous nerves of the spinal cord, or they may all be represented in a single large nerve, like the optic and olfactory. Thus it happens that some nerves, like those last mentioned, are "pure" nerves, while others, like the facialis or vagus, are "mixed," containing in some cases as many as four anatomically distinguishable components.

It is a general rule that in the body the components tend to be distributed among a large number of nerves in a more or less segmental way, while in the head they tend to be concentrated into a few pathways, or only one, into the brain, an adaptation which presents obvious advantages for the simplification and unification of the secondary reflex paths from these primary centers.

Now, the central nervous system is, as we have already seen, primarily a mechanism to facilitate the reaction of the animal to impressions from without, in other words, to put the body in correspondence with the environment. Its structure is directly determined by the avenues of sense through which these stimuli come in and by the character of the responses to these stimuli which are necessary for the conservation of the organism. In view of the fact that we already possess a detailed knowledge of these peripheral nervous pathways, it is manifest that we have here a most favorable avenue of approach in an analysis of the inconceivable complexity of cerebral structure.

We must know in detail the possible reflex pathways in the brain for all olfactory, visual, gustatory responses, etc., in the vertebrate type, and then on the basis of such a functional subdivision of the brain the problem of the mechanisms of higher cerebral processes may be attacked with a reasonable hope of success. The investigation of the internal organization of the brain may be pursued in several ways:

I. The direct study of the human brain, both normal and pathological. On account of the enormous practical importance of neurology to both human psychology and pathology, research naturally turned directly to the human brain; but a more unfavorable starting point could not be found.

II. It is now generally recognized that the complex human brain can best be understood by finding first a simpler pattern such as is presented by one of the lowest vertebrates. Accordingly the phyletic method has dominated all recent neurological research. The brains of individual species are studied and monographed, particular attention being paid to the lower members of the vertebrate series in the hope of finding in them a schema or paradigm which can be followed upward through the comparative anatomical series and, after comparison with the ontogeny of higher brains, lead to a reconstruction of the phylogenetic history of the brain. While this method has been of great service, especially to such problems as can be approached from the study of external morphology, it is immensely difficult when applied to the histological problems, and as a matter of fact has not as yet taken us very far.

III. A third method, instead of taking an entire brain as the unit of research, concentrates attention upon a single functional system and seeks to get exhaustive comparative knowledge of it in many types. Starting with a fairly accurate and detailed knowledge of the functional systems at the periphery, we have simply to extend the lines of inquiry here blocked out for us.

This gives a type of problem which is much more approachable than the others. It is not so complex but more

intensive. Of still more importance are the facts that the anatomical data can be directly correlated by physiological experimentation, and the method is open to experimental control all along the line. Our degeneration methods open up possibilities here which are incomparably more valuable than the most precise anatomical observation.

And nature has performed for us a series of experiments which are in a sense the converse of our degeneration methods. The various sensori-motor systems are very unequally developed, some animals possessing one in a high state of elaboration, some another. If therefore we begin our studies on the visual system for instance, with animals such as most birds with very highly developed eyes, and then compare with animals with vestigeal eyes, it is evident that we have here a means of isolating the system for scientific study which has some points of superiority over artificial experimental methods. Fortunately within the group of fishes, whose brains are all constructed on a plan fundamentally similar, we have the most remarkable diversity in the degree of development of the several systems, so that this is a favorable starting point for this method, especially since the brain is composed almost wholly of the simpler reflex mechanisms without the complications which we find in mammals due to the enormous development of higher associational centers in the forebrain. Some fishes have huge eyes, some are blind; some have elaborate olfactory apparatus, some very slight; some show a marvelous hypertrophy of the organs of taste, or touch, etc. These organs are all open to physiological study and so the functions can be accurately determined. Then, having found the cerebral pathways for each system where it reaches its maximum development, we can more easily trace out the system in other types, and thus arrive ultimately at a full knowledge of its evolutionary history.

All scientific method is both analytic and synthetic. In the phyletic type of neurological method, these two processes are apt to be far separated and the observed facts may remain inert and relatively meaningless, because imperfectly understood, incoordinated. In our third type of method, on the other

hand, it is easier to correlate the data as we go along, the synthesis accompanies the analysis, and the possibility of experimental control should keep the student in closer touch with his guiding facts and discourage general speculation.

As a concrete illustration of the practical method of applying the doctrine of nerve components in the functional analysis of the nervous system, we may summarize briefly the progress which has been made up to date in the study of the gustatory system.

In man, as is well known, the sense of taste is not very highly developed. The peripheral organs, or taste buds, are situated chiefly on the tongue, those near its base innervated by the glossopharyngeal nerve, and those near the tip probably by the chorda tympani of the facial nerve. But the gustatory pathway toward the brain is very imperfectly understood and many points are still in controversy, while the central path is almost wholly unknown.

But in certain fishes, such as the carp and cat fish, this system of sense organs is enormously exaggerated. Taste buds are found, not only in the mouth, but all over the outer skin and barblets. Direct experiment shows that these fishes actually do taste with these superficial sense organs—unlike some people, their taste is not all in their mouth.

The experiments made on the cat fish (Ameiurus) show that these fishes seek their food by feeling for it with the barblets and by means of them they discriminate between edible and non-edible substances, that they habitually use both the sense of touch and the sense of taste for the purpose and that they can be taught to discriminate between tactile and gustatory stimuli applied to the skin and will turn and snap up savory substances and reject objects which feel like them but are devoid of taste.

The exact distribution of the gustatory sense organs has been determined and their nerves traced back to the brain. We get the gustatory reaction from the skin as described above in fishes which possess these cutaneous sense organs, and the reac-

tion is not obtained from fishes which do not possess such sense organs and nerves.

All of these cutaneous sense organs are innervated from a single nerve, the sensory root of the facial (corresponding to the portio intermedia of human anatomy), which is the biggest nerve in the body. The center in which this nerve terminates in the medulla oblongata is about as big as the entire forebrain, instead of being barely discernable by refined histological methods, as in the human body. And the secondary gustatory path, which in man is totally unknown, is the largest single tract in the brain, both in the cat fish and in the carp!

The primary gustatory center in the medulla oblongata is bilobed, the "facial lobe" receiving the gustatory fibers from the skin and the "vagal lobe" receiving those from the mouth. From these lobes there is both an ascending and a descending gustatory path. The latter passes down to the point where the medulla oblongata merges into the spinal cord and there terminates in a special nucleus which is intimately related to the funicular nuclei, a center for tactile sensations. Here the tactile and gustatory stimuli are coordinated and a common descending bundle (tertiary path) passes back into the spinal cord for the body movements necessary to turn toward the food object. The ascending secondary gustatory path extends upward to a big nucleus under the cerebellum, from which tertiary pathways extend forward and downward into the midbrain (chiefly in the inferior lobe), then backward by a descending path of the fourth order into the medulla oblongata to reach the motor nuclei of the cranial nerves.

We have already gone far enough into our analysis of these secondary and tertiary gustatory paths to make it perfectly safe to predict that all of the habitual gustatory reflexes which we have observed in these fishes can be followed anatomically through the brain for their entire extent. And since we have the strongest reasons for believing that the elementary reflex paths are essentially similar in mammals and fishes, we expect to find here an important guide for further research in human anatomy.

So the other sensori-motor systems may be severally investigated, beginning the attack in each case with some species low down in the vertebrate series in which this particular mechanism is highly developed, and then extending the research to higher and lower types.

We may ultimately hope for a subdivision of the brain which shall be both structural and functional, each organ or pathway being given its function or meaning in the system as a part of the machinery of keeping the body in vital, helpful contact with environing forces. The great morphological "head problems," such as the primitive metamerism and the subsequent marvelous kalaidoscopic changes in structure and function of the component segments, these must all be read through the medium of such an intensive study of these factors upon which all differentiation has in last analysis depended.

There is another point of view from which I have been somewhat interested to develop the implications of the doctrine of nerve components, that of scientific methology in general.

It is said that scientific explanation consists essentially in such an organization of facts that they may be generalized or included under certain laws or uniformities which permit a forecasting of future events. Now, without going into an exposition at this time of the implied philosophy of nature, I think that a little reflection will show that this statement, while true in a certain limited sense, is very defective.

What is the nature of this organization of facts from which so great benefits are expected to flow? Can it in last analysis be anything other than the correlation of experience? All of the "facts" with which we deal have grown up in experience; they are in a literal sense the products of our experience. As men of science we have nothing to do with "things-in-themselves," only with phenomena, out of which we have constructed by mental process certain objective things which we regard as real—"constructs," or in common parlance, objects, facts, data.

By these things which grew up in experience (we have in most cases forgotten how) we measure up and evaluate all new

experience. If the new sense presentation is a yellow dog with white feet we assimilate it at once with previous experience and approve it as a valid fact. If, on the other hand, it is a green dog with thirteen scarlet heads each with a forked tongue, we are apt to ask, Am I awake or asleep? or, What was I drinking last night? Such an experience may be vividly real to me, but if awake and sane I do not accredit it as an object of sense, as a *fact* of experience, unless I can correlate it with the body of fact already approved.

But scientific laws are merely "facts" of wider import, which rest on a foundation of broader experience such that, when objectified, they remain not as concrete elementary experiences but as general categories including many such elements. The scientific generalization or law must therefore be approved or evaluated in a way strictly analogous with that by which we test sense impressions; that is, to be acceptable it must fit in harmoniously with the whole content of experience—"it must explain all the facts."

In the solution of any scientific problem that method is most likely to lead directly to fruitful results, other things being equal, which favors the correlation of the data all along the line so that each correlation may become at once a datum for future research, instead of reserving the major correlations until near the end of the investigation. And in biological research, to return to our text, we must not forget for an instant that the organism is a *functioning* mechanism. We cannot hope to understand any animal or plant or organ until we have an exhaustive knowledge of how it works. The anatomical fact is dead and inert unless it is vivified not only by the "salt of morphological ideas" as it was so happily phrased years ago, but also by the fresh warm blood of functional explanations.

Anatomy has given place, within the memory of even the younger generation of biologists, to morphology, in which the explanation is indissolubly linked with the fact. Nor can we stop here. No anatomical fact is complete until its physiological significance is added thereto. Like the old-time descriptive anatomist, the "pure" morphologist (or shall we dubb him

"poor morphologist"?) has no longer any tenable standing ground. What I mean is that anatomical structure cannot be understood as the morphology of today demands that it must be understood without a full knowledge of the functions of the parts, and we must know evolution of function before we can have true knowledge of the evolution of structure. And as a matter of fact the biological public is just now coming into a practical realization of the truth that we must have a comparative physiology parallel with our comparative anatomy. It seems to us now very strange that we have had to wait a whole century after the birth of comparative anatomy for even the beginnings of a realization in practice of this elementary principle.

That researches in descriptive anatomy and in pure morphology are still necessary and will continue to be called for to the end of the age there can be no doubt; but it is important that we remember that no study of structure is complete until the whole significance of that structure (including the evolutionary history of both its form and its function) is exposed and the whole complex of fact and meaning not only woven together into a single fabric, but fitted into the great pattern of reality as a whole in its proper place.

Now, no one of us can do this perfectly and, as time advances and the totality of the known becomes ever more vast and intricate, the difficulty grows apace. And yet this we must do in some measure in so far as we hope to rank as real builders in the permanent temple of truth. If we find ourselves unable to see the whole edifice in its proper perspective (as indeed who can?) we can at least build harmoniously with that nitch in which we find ourselves. Let no man delude himself with the idea that he is building for himself alone, that he builds on no other's foundation or that he can with safety ignore the labors of his coadjutors. Let no research worker hedge himself about and work in isolation; harmonious cooperation is the only possible way to get that breadth of view which all lack as individuals.

In our work on the nerve components we have endeavored to live up to these ideals. In so far only as we succeed in effecting wide and stable correlations from both the anatomical and the physiological side can we hope to be able to build a structure which shall endure as a secure foundation for an ultimately complete functional subdivision of the nervous system.

COLUMELLA AURIS AND NERVUS FACIALIS IN THE URODELA.[1]

By B. F. Kingsbury.

The following communication sets forth the results of a study made upon the relations and development of the parts in the otic region of the head in Necturus maculatus, and in comparison with that form, Desmognathus fusca and Spelerpes bilineatus.

The need for a careful study of (1) the relations of the facial nerve to the columella auris in the various Urodela, and (2) the homology of the suspensorio-opercular connections in the different forms of Amphibia has been emphasized by Gaupp.[2] From a comparison of the statements of Wiedersheim,[3] Huxley,[4] Parker,[5] and Hasse[6] he was lead to conclude

[1] This may be considered as a partial preliminary communication upon the development of the skull of Necturus maculatus, undertaken at the suggestion of Professors Wiedersheim and Gaupp, in the Anatomisches Institut at Freiburg. I wish to acknowledge my indebtedness to them and to Professor Keibel and others, for suggestions and material. Since the completion of this manuscript in May 1902, more than a year has elapsed, and in sending it to the press now, I take the opportunity of noticing papers that have appeared in the meantime—those of Kingsley and Coghill.

[2] '98, Gaupp, E Ontogenese und Phylogenese des Schalleitenden Apparates bei den Wirbeltieren. *Merkel u. Bonnet, Ergebnisse d. Anat. u. Entw.*, 1898, Bd. VIII, pp. 989–1149.

[3] '77, Wiedersheim, R. Das Kopfskelet der Urodelen. *Morph. Jahrb.*, Bd. III, pp. 352-548.

[4] '74, Huxley, Th. H. On the Structure of the Skull and the Heart of Menobranchus lateralis. *Proc. Zool. Soc.*, 1874.

[5] '77, Parker, W. K. On the Structure and Development of the Skull in the Urodelous Amphibia. Pt. I. *Philos. Trans. Roy. Soc.*, Vol. 167, Pt. 2.

'82a, On the Morphology of the Skull in the Amphibia Urodela. *Trans. Linn. Soc.*, Ser. 2, Vol. II.

'82b, On the Structure and Development of the Skull in the Urodeles. *Trans. Zool. Soc.*, London, Vol. XI, pp. 171-214.

[6] '73, Hasse, C. Ueber den Bau des Gehörorgans von Siredon pisciformis und über die vergleichende Anatomie des Kiefersuspensorium. *Anat. Stud.*, Bd. I, No. XV.

that there were apparently two methods of connection of the operculum with the suspensorium (quadratum). Thus, WIEDERSHEIM gives as the universal condition, that the nervus facialis passes *above* the suspensorio-opercular connection ; HUXLEY described a suspensorio-stapedial (opercular) ligament *under* the facial nerve; HASSE, in Siredon (Amblystoma) described the nerve as under the columella; while the statements of PARKER are not always clear, though it is evident that in the different Urodela both relations of columella or suspensorio-opercular ligament and nerve were described.

The study of the relations in the three forms above mentioned, to which Proteus anguineus, Amphiuma means, and Amblystoma tigrinum (larva) may be added, has shown that in all except Necturus, the nervus facialis passes below (ventrad to or cephalad of) the suspensorio-opercular connection. In Necturus, the ramus jugularis facialis passes above (dorsad to) the ligament, the remainder of the nerve, i. e. ramus mandibularis externus and internus, and ramus palatinus being below (ventrad or cephalad to) this structure. Furthermore, in these three forms, the columella or ligament passes from the operculum to the bone which lies partly upon the ear capsule and partly upon the external surface of the quadratum—and which, as far as I can judge from the evidence at hand, I regard as a squamosum ;—and not (primarily) to the cartilage of the quadratum as heretofore stated. This is a fact of considerable morphological importance. A more detailed description of the relations in the forms follows :

Necturus Maculatus. In this form HUXLEY[1] described the "suspensorio-stapedial ligament" as arising from the "middle of the posterior edge of the quadratum—and passing upwards and backwards to the stapes. The Hyomandibular branch of the seventh nerve passes passes above this ligament to its distribution just as it passes above the columella auris in the Frog." WIEDERSHEIM made no different statement of relations. This structure described by HUXLEY, which was presumably a sheet of

[1] Op. cit. p. 192.

fascia, is not the true suspensorio-opercular connection, which is correctly described by COPE,[1] as passing from the operculum to

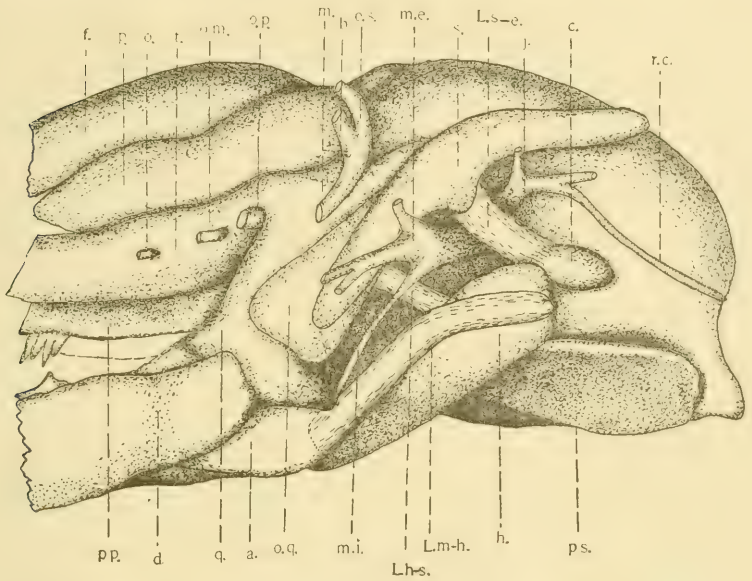


Fig. 1. Diagram from a drawing of the left side of a model of the skull of a Necturus 49.5 mm. long.

a.—Os articulare ?). *b.*—Nervus buccalis.
c.—Columella (operculum). *d.*—Os dentare.
f.—Os frontale. *h.*—Ceratohyale.
j.—Ramus jugularis VII.
L. h.-s.—Ligamentum hyo-suspensoriale.
L. m.-h.—Ligamentum mandibulo-hyoidale.
L. s.-e.—Ligamentum squamoso-columellare.
m. e. VII.—Ramus mandibularis externus facialis.
m. V.—Nervus maxillo-mandibularis trigemini.
m. i.—Ramus mandibularis internus facialis.
o.—Nervus opticus. *o. m.*—Nervus oculomotorius.
o. p.—Ramus ophthalmicus profundus trigemini.
o. q.—Os quadratum.
o. s.—R. ophthalmicus superficialis facialis. *p.*—Os parietale.
pp.—Os palatopterygoideum. *ps.*—Os parasphenoideum.
q.—Quadratum. *r. c.*—Ramus communicans glossopharyngei.
s.—Os squamosum. *t.*—Trabeculum.

the squamosum, who does not however, give the relation of the nervus facialis. DRÜNER has recently described correctly the relations in both Necturus and Proteus.

[1] COPE, E. D. The Batrachia of North America. *Bull. U. S. Nat'l. Museum*, No. 34, 18.

The following description of the relations in a Necturus of 49.5 mm. length, based in part on a model of this stage (Fig. 1), will serve as a basis of comparison. The operculum at this stage is roughly oval in outline and slighly ridged along its long axis. At its cephalic end it is fused with the otic capsule, projecting backward into the fenestra vestibuli. From the cephalic end a dense ligament passes cephalad and dorsad to the os squamosum at about its middle point. The bone forms a slight curve, the convexity looking upwards, and it lies upon the external semicircular canal of the otic capsule, extending down over the otic process of the quadrate and becoming closely connected with a bone lying upon the external surface of the quadratum, and which it partly covers. This bone[1] I shall describe in another place. The squamoso-opercular ligament is attached to the under side of the squamosum where the bone passes from the ear capsule to cover the outer side of the processus oticus quadrati. At this stage the "stapedial" process of the squamosum present in the adult has just begun to develop. The ligament, in its course from the operculum to the squamosum, passes external (laterad) to the ramus jugularis facialis and the vena jugularis. The ramus jugularis passes outward and slightly backward, between the ligament and the vein to the dorsal edge of the former where it receives the ramus communicans glossopharyngei, which lies close to the ear capsule laterad to the vena jugularis. Beyond the point of the union with the ramus communicans, the jugular branch of the seventh passes outward, under the ventral edge of the squamosum to curve around the dorsal side of the otic division of the M. depressor mandibuli. The ramus mandibularis externus facialis from its ganglion which lies immediately outside the foramen for the facial nerve, in a depression just caudad of the

[1] This bone arises in Necturus as a separate ossification, whose lower end subsequeutly is fused with or becomes the ossification of the quadrate. In Desmognathus and Spelerpes the same bone lies farther back, projecting under the squamosum, and in the adult forms the process of the quadrate named for the purposes of this paper the subsquamosal process.

processus basilaris quadrati, passes forward and outward under the quadratum to the outer surface of the squamosum, passing in front of (ventrad and cephalad to) the ligament.

The ramus palatinus which passes forward through a foramen distinct from that for the rest of the facial nerve, and the ramus mandibularis internus which passes immediately ventrad from the cephalic edge of the accessory lateral line ganglion, do not come into close relation to the columella, but are, of course, morphologically below and in front of it.

In an older Necturus, 9.4 c.m. long, the relations are as in the specimen just described, save that the processus "stapedialis" of the squamosum has attained an appreciable length, and the operculum possesses a short ossified stalk to which the liga-

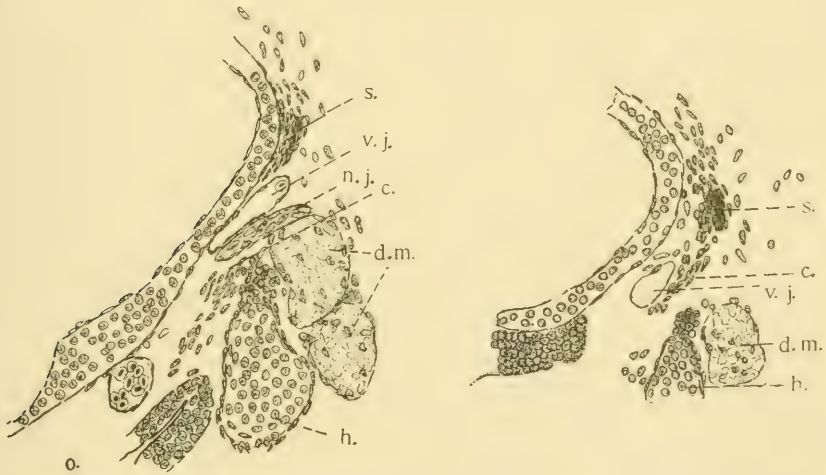


Fig. 2a. Section of the Necturus embryo 19 mm. in length. *c.*—anlage of the squamoso-columellar ligament; *h.*—hyoid; *v. j.*—vena jugularis ; *n. j.*—nervus jugularis ; *d. m.*—M. depressor mandibuli ; *s.*—squamosum.

Fig. 2b. Same, three sections farther forward.

ment attaches. Neither ossification appears to be an ossification of the ligament, but ossifications of the squamosum and operculum at each end of the ligament, acomplishing in that way the increase in length due to growth. In the adult, the operculum possesses an ossified process of some length joined

by ligament to the relatively long stapedial process of the squamosum.

That the relation of ligament to squamosum is a primary condition in this form and not a secondary modification, is seen in tracing the development of these structures. In an embryo 19 mm. in length (Fig. 2), the ossification of the squamosum is just beginning as a formation in a group of cells located upon the external semicircular canal of the ear. It extends down over the otic process of the quadratum covering with its lower (cephalic) end the upper end of a bone which is developed upon the external surface of the quadrate. At this stage, the operculum is just beginning to chondrify as a distinct center, and from it a cord of cells is continued forward, ventral to the vena jugularis and the ramus jugularis, to the cell surrounding the developing squamosum, becoming continuous with them a short distance (50μ) back of the processus oticus quadrati. The cells are of course continuous with those of the squamosum and also with the cells between that bone and the quadratum, so that the squamosum, the quadratum, and the ligament-anlage, may be said to be joined together by a common mass of cells. In the just hatched larva, likewise, the ligament-anlage, clearly goes to the under side of the squamosum and inserts itself between that bone and the processus oticus quadrati, so that it might be interpreted as going to both structures. As soon as the connective tissue fibers develop, however, the relation is seen to be with the squamosum and not with the quadratum. It is interesting to note the relatively early development of the ligament —practically at the same time as the squamosum and the operculum—later, however, than the chondrification of the chondrocranium.

Spelerpes bilineatus. In this form, as well as in Desmognathus, the suspensorio-opercular connection possesses the same relation to the nervus facialis—that is, the nerve lies entirely cephalad and ventrad to the stilus columellae; in other words, under it. In relation to the jugular vein, the stilus possesses the same relation as the ligament described in Necturus—i. e. it passes ventrad to it.

In the adult Spelerpes (Figure 3), the stilus is cartilaginous with a perichondral ossification continuous with the ossification of the operculum;—the cartilaginous core of the stilus, however, is distinct from the ring of cartilage within the operculum.

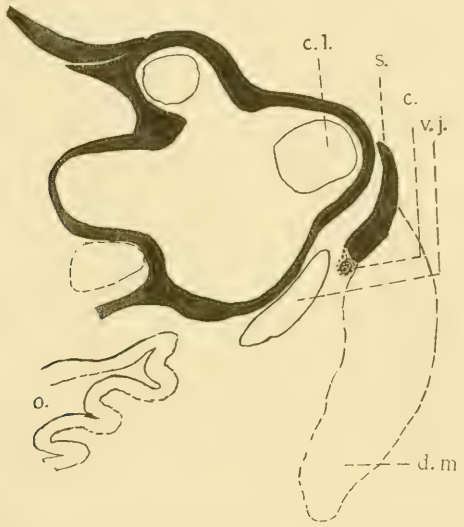


Fig. 3. Spelerpes bilineatus, adult 67 mm. long. Section through the right otic capsule. *c*—Stilus columellae; *o*—oral cavity; *v. j.*—vena jugularis; *d. m.*—M. depressor mandibuli; *S.*—squamosum.

The stilus passes forward, upward and slightly outward to the lower edge of the squamosum with which its cephalic end is joined by connective tissue (Fig. 3), and also with a small cartilage which lies upon the ventral edge of the squamosum. This cartilage extends forward for about 150 microns and is cylindrical. It is free at its caudal end, which articulates with the stilus, and fused with the ventral edge of the squamosum. The stilus and operculum are at about the same level. The former lies at first upon the dorsal side of the external semicircular canal, gradually moving down to the lateral surface of the otic capsule, as it is traced forward. As it continues to

shift its position ventrally to pass to the outer surface of the quadratum, it becomes farther separated from the ear capsule leaving a space in which the quadratum appears. The ventral (lateral) edge of the squamosum is thin where the bone rests upon the ear capsule, but becomes thicker as the bone leaves that structure, i. e. where the stilus articulates with it, becoming thinner again as the bone applies itself to the quadratum.

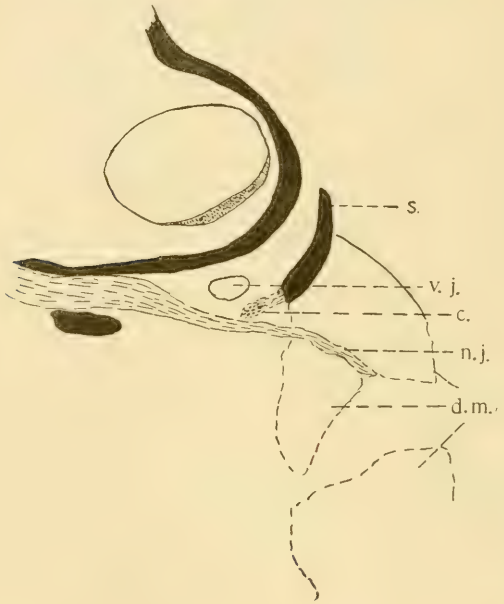


Fig. 4. Larval Spelerpes bilineatus, 43 mm. long; *c.*—stilus columellae; *v. j.*—vena jugularis; *n. j.*—nervus jugularis; *d. m.*—M. depressor mandibuli; *s.*—Squamosum.

In the interval between the squamosum and the ear capsule, two processes of the quadratum extend backward, (1) a bony process applied immediately to the inner surface of the squamosum, extending back to the level of the cephalic end of the cartilage upon the ventral edge of the squamosum, and (2) a short cartilaginous process lying between the bony process and the ear capsule. The latter seems to be a part of the (morphologically) basilar process of the quadratum and is very short.

Neither one comes into relation to the columella as do the corresponding processes in Desmognathus.

Larval Spelerpes of 25 mm., 35 mm., 43 mm. (Fig. 4) and 60 mm. in length, were examined in this connection and showed that the relation between columella and squamosum in this form (Fig. 4) is a primary one, as in Necturus. In the 25 mm. larva, the suspensorio-opercular connection is represented by a cord of cells which passes from the operculum forward and upward to the ventral edge of the squamosum. This cell cord lies ventrad to the vena jugularis around which it curves, closely applied to the vein, compressed between it and the R. jugularis facialis, the relation of nerve and suspensorio-opercular connection being thus the opposite of that in Necturus. Compare Figs. 2 and 4. In a 35 mm. larva cartilage has appeared in the cord of cells, otherwise the relations are essentially the same as in the younger larva, while in the 43 mm. specimen ossification of the stilus has begun, continuous with the perichondral ossification of the operculum.

The facial nerve, as has been said, lies entirely cephalad and ventrad to the suspensorio-opercular connection. The only branch which comes into contact with the stilus is the ramus jugularis which in the larva passes close to the ventral border of that structure. The ramus communicans glossopharyngei likewise, passes below the stilus, curving around it from its dorsal side in a course forward to join the facial. In the adult neither nerve is in as close relation to the stilus as in the larva.

The origin and significance of the small cartilage applied to the ventral border of the squamosum is obscure because of the absence of transforming and young adult material. In the larva it is not present.

With the exception of the R. jugularis and R. communicans, then, the suspensorio-opercular connection in Spelerpes has the same morphological relations as the ligament in Necturus.

Desmognathus fusca. (76 mm.) In this form it would seem as if, as compared with Spelerpes, the suspensorium were

displaced backward in relation to the operculum, so that the stilus is shorter, passes more directly outward and upward, and is joined more closely with the subsquamosal process of the quadrate (Fig. 5) than with the squamosum itself. It is,

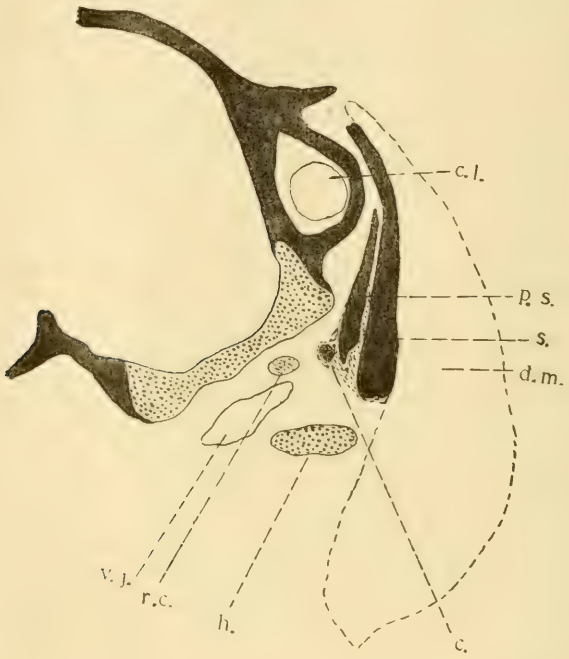


Fig. 5. Desmognathus fusca, adult, 76 mm. *c*—stilus columellae; *c. l.*—canalis lateralis; *h.*—hyoid; *v.* j.—vena jugularis; *r. c.*—ramus communicans; *d. m.*—depressor mandibuli; *p. s.*—subsquamosal process of quadratum; *s.*— squamosum.

however, joined to both bones by connective tissue, and with the cartilaginous process of the quadrate. This process is longer than the corresponding process in Spelerpes and is separated from the stilus by an interval of but (ca.) 50 μ (Fig. 6). The squamosum and the subsquamosal process of the quadrate are essentially the same as in Spelerpes. Stilus and operculum are as in Spelerpes, though the cartilage in the columella is small.

Turning to the larval form for an interpretation of the condition in the adult, we find in a specimen 21 mm. in length, that the suspensorio-opercular connection is at this stage cellular and extends from the cephalic border of the operculum to the squamosum as a dense cord of cells. It has the same rela-

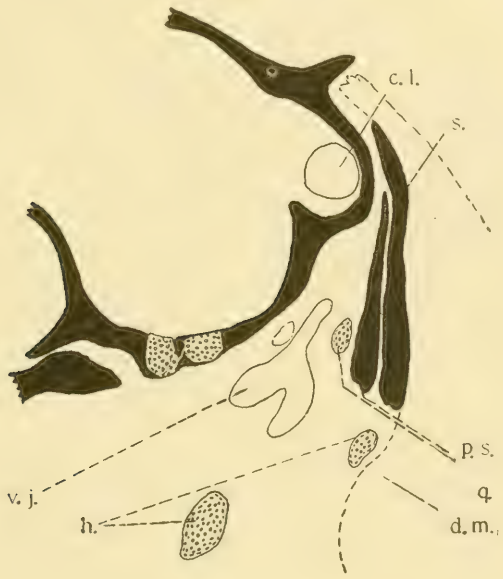


Fig. 6.¶ Same, three sections (75 μ) farther forward; *q*.—cartilaginous (columellar) process of the quadrate.

tion to the jugular nerve and vein as in Spelerpes, though it does not come into as close contact with either as in that form. Its cephalic end is rather difficult to determine (Fig. 7), since the anlage is continued forward to join the subsquamosal process (of the quadrate) which at this stage is a distinct bone, so that it may be said to be connected with both bones. There is, however, no direct connection with the (cartilaginous) quadrate, and from the conditions in Necturus and Spelerpes, we are warranted, I think, in emphasizing the connection with the squamosum rather than that with the subsquamosal process of the quadrate which, in fact, is not as direct. In a larva 33

mm. in length (Fig. 7), apparently approaching the period of transformation, the relations are as in the younger specimen save that cartilage has appeared in the suspensorio-opercular connection as a center distinct from the cartilage of the operc-

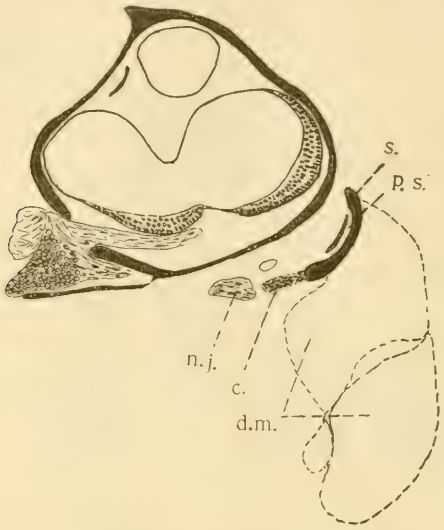


Fig. 7a. Larval Desmognathus fusca, 33 mm.; *c.*—stilus columellae; *v. j.*—vena jugularis; *n. j.*—nervus jugularis (R. communicans); *d. m.*—M. depressor mandibuli; *p. s.*—subsquamosal process of the quadrate; *s.*—squamosum.

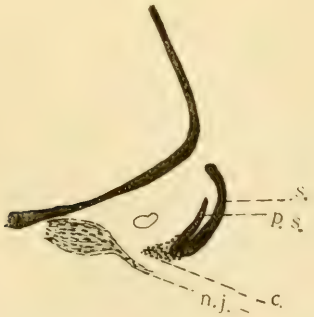


Fig. 7b. Same; three sections farther forward.

ulum. In a small adult (27 mm.), presumably but recently transformed, the cartilaginous stilus is connected more directly with the squamosum, but also by dense connective tissue with

the subsquamosal and the short cartilaginous processes of the quadrate. The shifting of the attachment takes place in the growth of the adult rather than at the transformation of the larva.

Amphiuma means (51 mm). Through the courtesy of my co-worker, Professor H. W. NORRIS, I am enabled to give here the following brief statement of the relations occurring in Amphiuma as found by him and verified by myself in his preparations. This form is interesting because it possesses a continuous cartilaginous connection between the quadrate and operculum, as described by WIEDERSHEIM,[1] HAY,[2] and WINSLOW.[3] This has been spoken of as the columella, and as the stapedial process of the quadrate. It evidently, however, represents both the columella (stilus columellae) and the primarily cartilaginous process of the quadrate found in Desmognathus. The articulation in the specimen upon which this statement of relations is based is much closer than it is in Desmognathus, and in older specimens undoubtedly, as described, there occurs a fusion of the two structures to form one continuous rod between the operculum and the quadratum. In this specimen, the stilus is a cartilaginous process of the operculum which is itself cartilaginous. The stilus columellae goes forward and slightly upward to become applied to the thickened ventral border of the squamosum to which it is joined by connective tissue. It is succeeded by the cartilaginous columellar process of the quadrate to which it is very closely connected. This process lies also against the ventral edge of the squamosum and slightly on its inner side. The connection of the stilus, therefore, is with the squamosum and the cartilaginous process of the quadrate and not at all with the ossification which (from the condition in the adult Desmognathus and Spelerpes) I have spoken of as the subsquamosal process of the os quadratum.

[1] Op. cit., p. 502.

[2] '90, HAY, O. P. The Skeletal Anatomy of Amphiuma during its earlier Stages. *Journ. Morph.*, Vol. IV.

[3] '98, WINSLOW, G. M. The Chondrocranium in the Ichthyopsida. *Tufts College Studies*, No. 5, 1898.

All branches of the facial nerve pass below the stilus columellae (and stapedial process of the quadrate) as has already been stated by HAY, instead of over it.[1]

Other Urodela. In Menopoma (Cryptobranchus) alone is the relation of columella to the squamosum described by WIEDERSHEIM,[2] and also by PARKER.[3]

In *Amblystoma* I can only state that there is present in the larva a cord of cells, passing from the operculum to the ventral border of the squamosum, which from the position and relation (dorsal) to the facial nerve is undoubtedly the anlage of the suspensorio-opercular connection. This relation of the "columella" to the facial nerve, has already been affirmed by HASSE and PARKER.

Proteus anguineus. Opportunity for studying the relations in this form was afforded me by the generosity of Professor WIEDERSHEIM. As might be expected from the published figures (WIEDERSHEIM; op. cit., Fig. 19), the relations in Necturus and Proteus are the same. There is a strong squamoso-opercular ligament passing from the stapedial process of the squamosum to the short stilus columellae, and to this the branches of the facial nerve have the same relation as in Necturus; R. jugularis passes above the ligament, R. mandibularis externus below it.

Nervus facialis.[4]

Since the homology of the chorda tympani is closely connected with that of the relations and connections of the columella auris, the following brief account of the course of the branches of the facial nerve is offered. The relations of the nerve in the larvae only of Desmognathus and Spelerpes have

[1] This is also in accord with KINGSLEY'S description. (*Tuft's College Studies, No. 7, p. 305.*)

[2] Op. Cit., p. 502.

[3] Op. Cit., Pt. III, p. 184.

[4] The following names of the branches of the facial nerve are used: R. palatinus; R. jugularis (FISCHER); R. mandibularis internus (R. Alveolaris, FISCHER); R. mandibularis externus (R. mentalis, FISCHER).

been studied, as the changes at transformation introduce complexities unimportant in this connection.

Necturus (9.4 cm.). The ganglion geniculi is intra-cranial, in the beginning of what might be described as a short facial canal, adjoining and cephalad of the cephalic division of the auditory nerve. From this ganglion the ramus palatinus arises as a small nerve which passes cephalad and ventrad through a separate foramen, and goes cephalad at the side of the trabecula, finally passing ventrad between the parasphenoid and the pterygo-palatinum to the roof of the oral cavity. The remainder of the nerve passes laterad through its foramen and develops a second ganglion, which undoubtedly belongs to the R. mandibularis externus, a part of the lateral line component. At this ganglion the nerve divides into two branches, R. mandibularis facialis, and R. jugularis; the former divides, as soon as it leaves the ganglion into the Rami mandibularis externus and internus. The R. jugularis passes upon the caudal side of the ganglion and has but little if any connection with it. Its course is nearly directly laterad for a short distance, passing dorsad to the ligament between that structure and the jugular vein; beyond the ligament, under the ventral edge of the squamosum it turns ventrad and caudad around the dorsal border of the otic division of the M. depressor mandibuli to pass under the fascia covering the lateral surface of that muscle. At the lateral border of the M. mylohyoideus posterior, it passes to the ventral side of that muscle. It innervates the M. depressor mandibuli, ceratohyoideus, and mylohyoideus posterior. The Ramus communicans glossopharyngei passes forward from the ganglion complex of the IX and X and joins the R. jugularis just beyond the point where it emerges above the columella. The M. depressor mandibuli gains some at least of its innervation from fibers of the R. jugularis which pass back along the R. communicans. R. jugularis seems to be purely a motor nerve, though it is possible that it may have a small lateral line component.

The R. mandibularis externus goes cephalad, laterad and ventrad under the ventral border of the squamosum below (in front of) the point of attachment of the ligament curving

around to the outer surface of the squamosum. After giving a branch to the skin whose destination was undoubtedly the lateral line sense organs, it divides into two branches, one[1] passing farther caudad and mesad, so as to lie on the mesal side of the lower jaw, between the M. submaxillaris and the skin; the other passing to the outer side of the lower jaw. From these two branches, evidently the lines of sense organs called by me[2] gular, and oral (incl. angular) respectively, receive their innervation. It is possible that the gular division contains communis fibers as well as those destined for the lateral line organs. The M. submaxillaris I find to be innervated by the trigeminus (R. mandibularis internus V), in this supporting Miss PLATT[3] as against RUGE.[4] Both divisions are subcutaneous,—i. e. external to all skeletal and muscular structure.

The ramus mandibularis internus, separates from the R. mandibularis externus as it leaves its ganglion, and passes ventrad and cephalad, on the inner (ventral) side of the quadrate soon passing through the suspensorio-hyoid ligament. This is the condition in a specimen 9.4 centimeters in length. In younger specimens the nerve seems to lie on the outer side of the ligament, though very closely applied to it. Beyond the

[1] This is evidently the branch described by VON PLESSEN and RABINOVICZ (Die Kopfnerven von Salamandra maculosa im vorgerückten Embryostadium, 1891) as "Begleiter des R. hyoideo-mandibularis (h. m')"—Hyomandibularis accessorius. By some these branches have been incorrectly called Rami mandibularis internus (alveolaris) and externus. The homology of either of these nerves with the chorda tympani, suggested by HERRICK in his '94 paper (Amblystoma punctatum) and accepted by KINGSLEY '02, for Amphiuma, can, of course, hardly hold now. COGHILL calls these, Rami mentales externus and internus.

[2] '95, KINGSBURY, B. F. The Lateral Line System of Sense-organs in some American Salamanders, and Comparison with the Dipnoans. *Proc. Americ. Micr. Soc.*, Vol. XVII, 1895.

[3] '98, PLATT, JULIA B. The Development of the Cartilaginous Skull and of the Branchial and Hypoglossal-Musculature in Necturus. *Morph. Jahrb.*, Bd. XXV, 1898.

[4] '96, RUGE, G. Ueber das peripherische Gebiet des Nervus facialis bei Wirbelthieren. *Festschrift für Carl Gegenbaur*, 1896, pp. 195-348.

ligament, the nerve is on the inner side of the M. depressor mandibuli, MECKEL'S cartilage and the os articulare successively. It is separated by connective tissue from the mucous membrane of the mouth which it gradually approaches, lying on the dorsal (mandibular) side of the depression[1] between the hyoid and mandibular arches. At about the level of the caudal border of the eye, it divides into two branches, one of which continues forward on the inner side of the jaw, the other moves farther ventrad and mesad; both, however, become compressed between the M. submaxillaris and the oral mucous membrane of the floor on the mouth between the hyoid (tongue) and the mandible.

No communication occurs between this nèrve and the Ramus mandibularis internus of the fifth.

In the larvae of Spelerpes[2] and Desmognathus the relations of the four main branches of the seventh nerve are in general essentially as in Necturus. The Ramus jugularis, however, instead of curving around the dorsal border of the otic division of the depressor mandibuli as in Necturus, in Spelerpes passes through that division of the muscle, while in Desmognathus, it passes *under* the *entire* muscle. In both Desmognathus and Spelerpes it contains a cutaneous—undoubtedly lateral line—component which was not found in Necturus. As in Necturus the M. depressor mandibuli receives its innervation from fibers that accompany the Ramus communicans. The relation of both the R. jugularis and the R. communicans to the stilus columellae has been spoken of in connection with that structure.

[1] "The *R. alveolaris VII*, composed wholly of communis fibers, follows the posterior border of the suspensorium to the angle of the jaw. Along this part of its course, the R. alveolaris lies mesially of the hyo-suspensorial ligament, and anteriorly of the deep pharyngeal evagination which represents the embryonic spiracular cleft." '02, COGHILL, G. E. The Cranial Nerves of Amblystoma tigrinum. *Journ. Comp. Neurol.*, Vol. XII, p. 228.

[2] The branches and distribution of the facialis in the larval Spelerpes have been correctly given by Miss M. A. BOWERS: The Peripheral Distribution of the Cranial Nerves of Spelerpes bilineatus. *Proc. Am. Acad. Arts and Sci.*, Vol. XXXVI, 1900.

The Ramus mandibularis externus passes cephalad and laterad around the lower edge of the squamosum to its outer surface, where it divides into branches, as in Necturus, one of which curves ventrally over the outer surface of the M. depressor mandibuli and its tendon to run forward upon the ventral surface of the M. submaxillaris. The other division runs cephalad upon the outer side of the lower jaw. Both seem to be purely lateral line nerves.

The R. mandibularis internus separates from the externus at the cephalic border of the ganglion and goes laterad cephalad and ventrad immediately to the mucous membrane of the oral cavity between the hyoid arch and the quadrate and (farther cephalad) the mandible. In the first part of its course it lies in the connective tissue between the oral mucous membrane, the quadrate and the M. depressor mandibuli, the quadrate lying dorsally and the muscle laterally. Farther cephalad it passes on the inner side of the suspensorio-hyoid ligament, MECKEL'S cartilage and the os articulare on whose mesal side it divides, one branch passing through a canal in that bone to join the R. circumflexus V,[1] which at nearly the same level passes between the os dentare and MECKEL'S cartilage. This soon divides on emerging from its canal into the R. submaxillaris and R. mandibularis internus V. The remainder of the R. mandibularis internus VII runs forward between the mucous membrane and the mandible. At the level of the appearance of the M. submaxillaris, it is compressed between that muscle and the mucous membrane of the floor of the mouth. The portion of the R. mandibularis internus VII which joined the trigeminus I was unable to trace. I was unable to trace the fibers of the R. mandibularis internus in any of the forms even into the neighborhood of taste buds. It is clear, that the R. mandibularis internus (alveolaris) in Urodeles has practically the same course, the only marked differences being that in Necturus, and Proteus, it does not pass through a canal in the

[1] I use the name applied to the comparable nerve in the frog, believing them homologous. Compare, however, COGHILL, op. cit., pp. 265 and 266.

os articulare (angulare?), while in Amphiuma,[1] ('02, KINGSLEY), Desmognathus and Spelerpes, Amblystoma, Salamandra and Triton, (COGHILL, op. cit., p. 269), it occupies such a canal. In Necturus, Proteus, and Amphiuma (KINGSLEY) it does not anastomose with the Vth, while in the other forms it does.

From the above relations it is seen that the only nerve which can be considered as a homologue of the chorda tympani is the Ramus mandibularis internus VII which goes to the mucous membrane of the floor of the mouth between the hyoid and mandibular arches.[2] This, of course, is the homology already advanced by GAUPP,[3] STRONG[4] and others, GAUPP from morphological relations, STRONG from the character of the fibers and their destination. ALLIS,[5] HERRICK[6] and GREEN[7] have since seen reason to doubt the homology on the grounds of the pretrematic position which the homologue of the chorda tympani must have, the nerve identified by them as R. mandibularis internus facialis being a post-spiracular nerve, and a Ramus facialis pretrematicus being chosen by them as the homologue of the chorda tympani.

[1] '02, KINGSLEY, J. S. The Cranial Nerves of Amphiuma. *Tufts College Studies*, No. 7, pp. 293-321.

[2] RUGE (op. cit., p. 294) recognizes this nerve as the chorda tympani though he does not identify it as the internal mandibular (alveolaris, FISHER) but seems to find that also present as a cutaneous nerve. COGHILL (op. cit.) regards it as a homologue of the chorda tympani.

[3] '93, GAUPP, E. Beiträge zur Morphologie des Schädels. I. Primordial Cranium und Kieferbogen von Rana fusca. *Morph. Arbeiten* herausg. von G. SCHWALBE, Bd. II.

[4] '95, STRONG, O. S. The Cranial Nerves of Amphibia. A Contribution to the Morphology of the Vertebrate Nervous System. *Journ. of Morph.*, Vol. X.

[5] '97, ALLIS, E. P. The Cranial Muscles and Cranial and first Spinal Nerves in Amia calva. *Journ. of Morph.*, Vol. XII, No. 3, 1897.

[6] '99, HERRICK, C. J. The Cranial and First Spinal Nerves of Menidia; a Contribution upon the Nerve Components of the Bony Fishes. *Journ. Comp. Neurol.*, Vol. IX, 3-4.

[7] '00, GREEN, H. A. On the Homologies of the Chorda Tympani in Selachians. *Journ. Comp. Neurol.*, Vol. X, 4.

The question seems to me to involve the correctness of the interpretation of the chorda tympani as pretrematic, and the homology of the mandibularis internus VII, in Menidia, Amia and Selachia, which appears to have a course somewhat different from that of the branch in Urodeles. For a comparison of the relations in fishes and Amphibia, the effect of the morphological differences in the suspension of the jaw and the value of the relation of nerves to skeletal structures in determining their homology, are involved; and for the larger question of the chorda tympani, the homology of the sound-transmitting apparatus in the different classes, as well; so that it seems to me a close consideration of homologies is yet premature.

The pre- or post-trematic origin of the R. mandibularis internus in Urodeles cannot, of course, be determined, since the first gill cleft does not come to development. From its point of origin and course, it certainly could be pretrematic, as COLE[1] has pointed out, and it seems to me the possibility that this nerve represents a pre-trematic nerve such as GREEN, (e. g.) described in Selachia,[2] is worth considering. In this connection the different relations of the facial nerve and columella auris in Anura and Urodela must also be considered. There is here presented in allied forms, a difference of relation

[1] '96, COLE, F. J. On the Cranial Nerves of Chimaera monstrosa (Linn) with a Discussion of the Lateral Line System and of the Morphology of the Chorda Tympani. *Trans. Roy Soc.*, Edinburgh, Vol. XXXVIII, Pt. III, (No. 19).

[2] I have already referred to the statement by COGHILL (p. 228) that this nerve could be considered pre-trematic. In the forms studied by me, however, the conditions, I believe, hardly warrant a definite conclusion. COGHILL, even, would regard the R. mandibularis internus in Urodela and Anura, as not homologous (p. 265), and this, too, seems to me rather extreme. The entire hyomandibular nerve in the frog crosses over and behind the columella auris and in Urodela under and in front of it. As stated in a previous paper ('95, The Structure and Morphology of the Oblongata in Fishes; *Journ. Comp. Neurol.*, Vol. VII, p. 30) where I quote also the opinion of Miss PLATT to that effect, I feel that the origin and distribution of a nerve are of more importance than its course, which may vary, and consequently should not be too closely made the basis of homologies. We also see that the relation of a nerve to a muscle cannot be relied upon as a test.

of nerve to skeletal structure of extreme type. As is well known,[1] in the frog the hyomandibular nerve crosses above the columella and passes down behind it to its destination, whereas in Urodeles it passes in front of or below the same structure. Other cases of similar differences of relation in this region, mentioned in this paper, are (a), the relation of the jugular nerve in Necturus on the one hand and in the other salamanders investigated on the other hand; in the first case it passes above the columella (stilus columellae), in the second, below. (b), Necturus also offers a difference in the relation of the internal mandibular branch to the quadrato-hyoid ligament. In Desmognathus and Spelerpes the nerve passes on the inner side of the ligament; in Necturus, through the ligament, or on its outer side in younger individuals. Further (c), the R. jugularis in Necturus passes over the depressor mandibuli; in Spelerpes larvae, through it; in Desmognathus larvae, under it.

The differences, in the last two cases at least, it seems to me, might possibly be explained on a more or less mechanical basis. The nerves (and muscles) are already developed and their course and positions established before the anlage of the columella or that of the quadrato-hyoid ligament has appeared, and the relations the latter structures assume when they do develop, has been determined for them by the position of the structures earlier developed. This explanation would not, of course, be an ultimate one.

The nomenclature employed in the above descriptions is that suggested by Professor GAUPP. *Columella*, including operculum and its process, *stilus columellae*, which may be joined to the suspensorium by an appreciable ligament—*ligamentum suspensorio-columellare* (*operculare*). I regard the suspensorio-columellar (opercular) connection in the forms studied as homologous. The term stilus columellae is used in describ-

[1] '93, GAUPP, E. Beiträge zur Morphologie des Schadels. I. Primordial Cranium und Kieferbogen von Rana fusca. *Morph. Arbeiten*, herausgegeben von G. Schwalbe, Bd. II.

'99. ECKER'S u. R. WIEDERSHEIM'S Anatomie des Frosches, auf Grund eigener Untersuchungen durchaus neu bearbeitet. II Abth. 1899.

ing the relations in Desmognathus and Spelerpes, in view of the structure in the adult, despite the fact that the "stilus" probably begins as a chondrification in the cord of cells extending from the operculum to the squamosum. This point of a separate chondrification, however, has not been firmly established. In that case the ligamentum squamoso-columellare (operculare) and the stilus columellae of Spelerpes I should regard as homologous—despite the different relations to the facial nerve.

In conclusion, I may say that the points which I wish to emphasize are:

(1) The primary connection of the columella with the bone which I regard as the squamosum.

(2) The different relations of the facial nerve to the ("squamoso-opercular" connection) stilus columellaris in the frog, Necturus (and Proteus) and other Urodela.

(3) The secondary nature of the connection of the columella with the quadrate cartilage, where such connection occurs.

(4) The different relations of the ramus jugularis VII, to the musculus depressor mandibuli in Necturus, Spelerpes, and Desmognathus.

(5) The course and relations of the R. mandibularis internus VII, in view of the possible homology with the chorda tympani.

(6) The question of the value of the relation of a nerve to skeletal parts and muscles, as a criterion of homology.

Anatomisches Institute, Freiburg i. B., May 1, 1902.
Cornell University, Sept., 1903.

EDITORIAL ANNOUNCEMENT.

The Journal of Comparative Neurology, as originally announced, was open to contributions in the field of comparative neurology, physiology and psychology. The founder, feeling that the time was ripe for a more thorough correlation of the facts in these different fields, planned to devote the Journal as much to the functional as to the structural study of the nervous system. During the thirteen years of the existence of the Journal of Comparative Neurology, the functional side of neurological work, although not wholly neglected, has received far less attention than was originally contemplated, chiefly on account of the continued ill-health of the Editor-in-Chief, who had intended to devote himself primarily to comparative psychology.

Now, however, we are able to announce an enlargement of the editorial staff which will insure a more satisfactory representation of the functional as well as the structural aspects of neurology.

The Journal will hereafter be known as the "Journal of Comparative Neurology and Psychology." The organization of the editorial staff remains in general as before save that Dr. Robert M. Yerkes of the Department of Psychology, Harvard University, will be the responsible editor for the department of Animal Behavior. He will be supported on the editorial board by representative students of Comparative Psychology and other departments will be strengthened by the addition of collaborators.

The attention of psychologists, physiologists and medical practitioners is called to the fact that this is the only journal in any language especially devoted to this large and important field of research. It is our aim to make the Journal indispensable to all interested in the structure and functions of the ner-

vous system from whatever point of view. They will find much of value in the materials published, for in addition to the recognized fact that the human nervous system can be best understood structurally by a study of its phylogeny, it is now clear that an understanding of the reactions of lower organisms and especially of the evolution of action, is necessary for an appreciation of the functional significance of the human nervous system.

For morphologists the Journal will continue to be, as in the past, the *vade mecum* in its department. And we again call attention to the fact that by comparative neurology we mean not the study of the nervous system of lower organisms alone, but all neurological researches carried on in the comparative spirit and by the comparative method.

In addition to technical articles of a special nature, there will be presented critical digests, synthetic reviews and editorial summaries of particular topics designed to give in a non-technical way the most important results of research in each of the specialties in our field.

Hereafter the Journal will appear bi-montly, and each annual volume will contain about five hundred pages. The first number of the new volume we hope to have ready in February. Every effort will be made to secure as prompt publication of acceptable contributions as is consistent with the high standard of scientific and mechanical excellence which we propose to maintain.

The subscription price will be $4.00, strictly net (foreign subscriptions $4.30, 18 s., M. 28, 22 fr., L. 22). All MSS. and matter for review should be sent to the responsible editors. Those dealing with the structure of the nervous system and all business correspondence should be sent to the Managing Editor, C. JUDSON HERRICK, at Denison University, Granville, Ohio; those dealing with the functions of the nervous system and comparative psychology may be sent directly to Dr. ROBERT M. YERKES, Psychological Laboratory, Harvard University, Cambridge, Mass.

LITERARY NOTICES.

The Relations of Biology and Psychology.[1]

The book before us has already been reviewed by a number of writers and needs no introduction to the readers of this journal. The purpose here is simply to touch upon certain points (not dwelt upon at length by any of these reviewers) which are of interest at once to the psychologist and to the biologist.

(1) Psychophysical Evolution. The papers which are here gathered together may be treated, says the author, "as each dealing with a narrower question, yet as having reference to the larger problem which may be called *psychophysical evolution*—the evolution of mind and body together" (p. 2). This conception of psychophysical evolution is one to which the author returns again and again throughout the book in a way which is stimulating or exasperating according to where the reader stops in in the perusal of the book.

One at first feels that the author has struck out the true solution of a perplexing question, and he turns the pages expectantly until he shall come to the convincing presentation of this great thought. But as he proceeds all that he finds is the cheerful assumption that this has already been made as clear as is necessary—and this is the source of the feeling of exasperation.

The clearest brief statement of the principle of psychophysical evolution is that in which the author says that "the brain not a brain when consciousness is not there," and "consciousness does not, on the other hand, produce movement without a brain" (p. 130). This most promising suggestion leads the reader to the natural conclusion that the author has in the background a point of view which justifies what appears upon the surface as a rather paradoxical juxtaposition of concepts usually kept quite distinct. What is this point of view?

We all, doubtless, today, feel that brain and consciousness are equally genuine and valid phases of the reality of experience; and

[1] BALDWIN, J. MARK. Development and Evolution: Including Psychophysical Evolution, Evolution by Orthoplasy, and the Theory of Genetic Modes. *The Macmillan Co., New York*, 1902.

this has been stated in many metaphors and similes. We are all either asking the question "why the mind has a body" or why the body ever came to have a mind. But what we still lack is an analysis of the origin and meaning of the distinction—its genesis and its function. Why do we distinguish between brain and consciousness at all, if ultimately they are so intimately one? Just how is their difference related to their identity? How did the distinction originally come to be set up, and what modifications has it undergone in the history of scientific thought?

(2) The Psychological and the Biological. The author's discussion of the terms "psychic" and "psychological" (Chap. I, §2) is a hint of such an analysis. In this section Professor BALDWIN distinguishes between the "pyschological" and the "psychic" as follows: "By the psychological I mean the mental of any grade, *viewed from the outside;* that is, viewed as a definite set or series of phenomena in a consciousness, recognized as facts and as 'worth while' as any other facts in nature." "This occurrence of a psychological change in an animal is a fact in the same sense that the animal's process of digestion is" (p. 4). "The discussion of the respective spheres of these two sciences turns upon a distinction of points of view. On the one hand the psychologist as such, and for his science, must aim at the recognition only of the facts which are psychic or mental; that is, of such as are facts to the consciousness *in which they occur*. These alone are psychic, and these belong to individual psychology" (p. 5). "Psychology, when considered as the science of mind,—that is, looked at from the objective point of view,—takes cognizance of the 'psychonomic'; but when considered as a subjective science, as interpreting its own data, it does not; but, on the contrary, it confines itself to the psychic" (p. 8).

By way of criticism of this, the question at once arises whether there is any such thing as psychology "considered as a subjective science"? Many other writers have been insisting that there is no "individual psychology" in this sense; there is no science of the individual. From this point of view, the "psychologist as such" is no scientist at all; the attempt to draw a distinction between two kinds of psychology in this sense proves suicidal. If the difference "turns upon a distinction of points of view," then it does not turn upon a distinction of contents; if it is a distinction of method only, then it is not a distinction of subject-matter. When we take up "the standpoint of the observer, that of the scientific man who essays to investigate *some one else's consciousness*, or that of an animal,

the procedure is now subject to different rules and limitations" (p. 5) it is true, but this is essential to any science of psychology; this is not another kind of psychology over and above so-called "individual psychology." Individual psychology is not scientific psychology apart from this. There is no *science* of psychology which deals with the strictly *psychic*.

Moreover, this view gets the author into difficulties when he comes to apply it to his doctrine of psychophysical evolution. "But now, and this is the essential point to remark in our present connection, so soon as we ask the psychophysical question of genesis,—that of the development and evolution of mind and body taken together,—pursuing the biogenetic method, this limitation no longer rises to trouble us. We include all psychophysical facts as such in the definition of our science. Changes in mind and body go on together, and together they constitute the phenomena. Both organic and mental states and functions may be appealed to in our endeavor to trace the psychophysical series of events of such, since both are objective to the spectator, the scientific observer" (p. 8). Accordingly, "with the general understanding now arrived at, we may take a preliminary survey of the field in the light of certain current hypotheses. Among these is what is known as 'psychophysical parallelism'" (p. 10). "The principle of parallelism assumed, we claim once for all the right *to neglect the relation of the two terms, mental*[1] *and physical, in all circumstances whatsoever*" (p. 15).

But how can we interchange the psychical and the physical if, by definition, the psychic facts are facts only "to the consciousness in which they occur?" The law that "for science all facts are equal" does not mean that the physical and the psychical can be interchanged without changing the "point of view." And if the author here does not mean the psychical by his term "mental," then how does the discussion become relevant to the doctrine of psychophysical parallelism?

What Professor BALDWIN seems to mean is that the same process of psychophysical evolution may be stated either as psychological or as biological, i. e., it may be interpreted from either of these *equally objective* points of view. But this has nothing in common with the doctrine of psychophysical parallelism. The latter, as he says elsewhere, is a question of ultimate philosophical interpretation, while the former is a question of division of labor in scientific method. Not that the

[1] Note that the ambiguous term "mental," so important at this juncture, is not defined. Does the author here mean "psychic" or "psychological?"

question of methodology does not have an important bearing upon this question of the distinction between the psychical and the physical, but this relation can not appear as long as one member of the distinction is taken as fixed.

(3) The Place of Consciousness in Evolution. The place of consciousness in evolution is the same on either the Lamarckian or Darwinian view. This is made possible by the author's theory of organic selection and social heredity. One of his reviewers, indeed, thinks that he has not wholly escaped the fallacy of supposing that consciousness produces causal changes in the physical world of muscles. But, besides the author's disavowal of such a doctrine in a reply to this review, he distinctly says in the work before us that there is a third view beside the theory of automatism and the theory that consciousness is a *vera causa* (p. 121).

But what is this third view? Does the author here intend a functional interpretation of the relation of the psychical to the physical? If there is one psychophysical system, and if consciousness is simply the meaning of this system when it is tensional, as contrasted with the state of the same system when in the relatively stable equilibrium of habit, then consciousness can be included in the statement of the antecedent phenomena explanatory of a voluntary movement—not indeed, as a distinct phenomenon, but as the statement of a continuous process in one of its stages. To say that the same movement could take place without this state of consciousness is to say that the fact that it was a conscious movement (i. e., had this meaning as distinct, say, from an habitual movement) does not make it a different movement from one which is not conscious. Any mark or character of the movement makes it a different movement. In truth, no two movements are ever exactly alike. Of course, you may abstract from all these differences, but then your judgment is an hypothetical and not a descriptive one, and here the aim, as the author says, is to secure a scientific in the sense of a descriptive statement of the facts.

The suggestion that heredity rather than variation is the fact to be accounted for in evolution, "that variation is normal, and that heredity is acquired through the operation of natural selection restricting the limiting variation" (p. 230), is, then, to be put alongside of this other contention of the author, that consciousness, in one form, is the growing-point of evolution from the first. Is not this tantamount to saying that what we call consciousness is the variable element in development and evolution, that consciousness represents the shifting area of tension in adaptation, or, to put it from the other side, the moving

equilibrium, or struggle toward equilibrium, between the forces of the organism and the environment?

(4) Mind and Body. The problem of the relation of mind and matter, from this standpoint, becomes chiefly a question of the logic of scientific method. The present writer has elsewhere (*Philosophical Review*, May, 1903) suggested that this is the consistent interpretation of Professor BALDWIN's chapter, in the book before us, on "Mind and Body." The psychical ceases to be an entity in any sense of the term, even in the sense of energy. Instead of the psychical being subordinated to the concept of energy, as Professor OSTWALD contends, or being regarded as interchangeable because universally parallel, as Professor BALDWIN contends, these concepts must, in time, be reconstructed in terms of each other, and take their place in a scientifically continuous series, the terminology of which remains to be worked out, but of which it is the great distinction of Professor BALDWIN to have given a hint in his otherwise paradoxical doctrine of psychophysical evolution. Another hint in the same direction is the recent attempt to define the meaning of the psychical by Professor GEORGE H. MEAD, in the University of Chicago Decennial Publications, Volume III, where the psychical is defined as the process, as contrasted with the content, of the experience, or, to use the terms of logic which he employs, the psychical is identified with the copula of the judgment.

H. HEATH BAWDEN.

The Psychology of Action.[1]

We have in this book what we have learned always to expect from the pen of its distinguished author, a lucid, interesting and original presentation of the principles of psychology. Its originality consists in the successful employment of terms chosen from the sphere of practical life, as the leading categories and principles of division. Instead of the traditional classification of the subject-matter under the rubrics of cognitive, affective, and conative states, we have the refreshing consciousness of feeling that we follow the meaning of the author from the beginning without being involved in a system of technicalities. He discusses mental life under the headings of Sensitiveness, Docility, and Initiative. These terms retain the content which they have in ordinary life while at the same time serving the purposes

[1] Outlines of Psychology; An Elementary Treatise with Some Practical Applications. By JOSIAH ROYCE, Ph. D., LL. D. *New York, Macmillan Co., 1903.* (In the Teachers' Professional Library series, edited by President NICHOLAS MURRAY BUTLER.)

of an accurate psychological analysis. The main discussion under these heads is preceded by four chapters entitled respectively: "Introductory Definitions and Explanations," "The Physical Signs of the Presence of Mind," "The Nervous Conditions of the Manifestation of Mind," "General Features of Conscious Life." The author then proceeds to discuss the three chief forms of *Sensitiveness*, viz: "Sensory Experience," "Mental Imagery," "The Feelings." The aim here is to "make a summary statement of the principal kinds of states of consciousness that occur within the range of our psychological experience," considered especially with relation to the sorts of physical conditions upon which they depend. *Docility* is treated in five chapters. This is the study of the "relations that bind the consciousness of any moment to previous experience." The "General Law of Docility" is the law of habit which is traced through its various exemplifications in "Perception and Action," "Assimilation," "Differentiation," and "Imitation," which introduces to us "The Social Aspect of the Higher Forms of Docility." *Initiative* is discussed in a single chapter entitled: "The Conditions of Mental Initiative." This is followed by two concluding chapters: "Certain Varieties of Emotional and Intellectual Life," "The Will or the Direction of Conduct."

In general standpoint this book may be regarded as a contribution to what is coming to be called the functional point of view in psychology. This is seen in the insistence upon the integrity of experience, in the valuable critique of the doctrine of conscious elements as employed by the structural psychologist, and in the use throughout of the biological conception of habit, and even of consciousness, as special developments within the life of the organism for the sake of enabling it to adjust itself in its changing environment. Probably the author did not have this last point so explicitly in his aim as might be inferred from the statement just made, but it is only the more significant if such is the case. Hints of it are scattered throughout the book without any more explicit statement being made than that embodied, for example, in the following sentences: "The central processes which our images accompany form themselves a part of our reaction to our environment, *and our more organized series of mental images actually form part of our conduct*" (p. 160).[1] "Thought is either action or nothing" (p. 351). Here is the gist of the functional point of view, that all the various forms of consciousness are special developments *within* action, and, therefore, special developments *of* action.

[1] Italics ours.

As this, to the present reviewer, is the most significent feature of the entire treatment, it may be instructive to show in what ways action is here made fundamental.

(1) The author says, "The single facts of sense, and the single movements which we make, are always related to, or, as one may say, are differentiations of our general orientation" (p. 147). This is connected with the "tropisms of orientation." "The reactions of orientation are among the most fundamental phenomena of healthy life." "Our sensory experience at any moment will stand partly for our more general activities of orientation, and partly for our more special reactions to individual objects" (p. 143). "The special acts are always superposed upon the general acts." "All our particular sensory experience will be related, not only to our special acts, but to our general acts of orientation, and to those experiences which result from these acts." "All such sensory experiences appear to our consciousness as facts existent within a certain primitive whole, which, apart from differentiation, is our experience of the general orientation of the entire organism" (p. 146). The author, in other words, is insisting that our motor or kinaesthetic experiences (sensations and images) form the very core of consciousness. The kinaesthetic sensations supply the fundamental imagery of meaning. This is equivalent to saying that action is the fundamental category of experience and the various forms of conscious experience are special developments within this. Here, by the way, was an excellent opportunity to clear away at a stroke the whole difficulty of the relation of the psychical to the physical, in so far as psychology is concerned, since consciousness here appears simply as action passing through a tensional or reconstructive stage. "Tension," he says on a previous page, "the mutual opposition and balancing of numerous tendencies, is absolutely essential to normal life." Why should consciousness any more than habit be hypostasized, if both are equally developments of action?

(2) The statement which the WEBER-FECHNER law receives is a good illustration of the tendency to interpret experience from the standpoint of the act, from the standpoint of the organic circuit, as the functional psychologists would say, rather than from the standpoint of any one of its contained minor activities. "The law is that in order that differences of sensory experience should have, in two different cases of comparison, the same value for our reacting consciousness, or should appear to be equal differences, the stimuli that are compared in the two different cases must differ from one another, not by the same absolute physical difference in their magnitude, but by the same

relative difference" (267-8). "The psycho-physic law appears now to formulate a certain limit to which the Docility of the organism in responding to finer differences in stimulation is subject" (270). That is, "the psycho-physic law is not a law directly relating to our sensations, but is rather a law of our reactions" (272).

(3) In chapter XII we have a most illuminating statement of the relations of thought to action in a discussion of the psychological and social functions of language. Thinking differs from naive action chiefly in this, that in thinking we reflect on the details of the action, and bring the method of the action to consciousness. "One who thinks makes it part of his ideal to be conscious of how he behaves in the presence of things. And this he does because the social comparison of his acts with the acts of other people not only controls the formation of his acts, but has made his observation of his own acts an ideal' (284). "The consciousness of how one performs the act" is the very essence of thought. The abstract idea or concept is a reduced act. Take the concept or "horse" or "man." "Whoever knows what a horse or man in general is, knows of some kind of act which it is fitting to perform in the presence of any object of the class in question." "The name 'man' or 'horse,' the word-image associated with any such subject, is itself a part of a well-known act by which one may react in the presence of an object in the class in question. For *naming objects* is *one way of responding to their presence*" (286-287). "Our general ideas . . . stand, therefore, for certain . . . attitudes." "Our mental images of outer objects are never to be divorced from our reactions." A "general idea is a conscious plan of action."

(4) The treatment of the relation of feeling to action supports the same general conception. On page 296 we read, "Like the thinking process in general, the reasoning process develops out of conditions which at the outset involve a very rich, and in fact predominant presence of feelings and of complex emotions. That is, reasonings have resulted from what were at first decidedly passionate contrasts of opinion." Thinking, reasoning, here would appear at the setting up of distinctions and the introduction of control within the primitive predominantly affective type of consciousness. In the chapter on the Feelings the author refers to the traditional view of the relation of feeling to thought and to action as embodying an important truth, but seems hesitant about adopting it. "Those who divide mental life, in the well known traditional way, into the life of cognition, the life of feeling, and the life of will, are accustomed to assign to the feelings a

stage intermediate between the life of cognition and the life of will. From this point of view our cognitive consciousness first furnishes to us the *facts*. In terms of our feelings we estimate the *values* of these facts for us. In view of these values our *acts* are determined. That this traditional view has a real significance cannot be questioned. But in the present exposition of the structure and laws of consciousness we are not at all closely following the lines of the traditional exposition" (164). Now the reviewer ventures to suggest that this traditional view, with one modification, stands more in line with the general method of treatment pursued in this book than does the exposition actually given. On another page (226), the author says that in ordinary association "the perception is relatively instantaneous." "The present sense disturbance is at once associated with a consciousness due to already established motor habits" (225). This suggests the real significance of the traditional view—which holds that we first perceive something, then feel interested in it, and then act upon it—only the traditional view regards this as a conscious act of perception, whereas, in truth, this initial perceptive act is automatic, instinctive or habitual. It is a good illustration of one of those "attitudes" to which the author refers elsewhere. The traditional view is true except that the cognition which comes first is not conscious or reflective but instinctive or intuitive. And the consciousness, which the author says accompanys our acts, or takes place "side by side with the tendencies to action" (164), from this point of view is rather developed within the action at the point where and because of the fact that this instinctive perceptive habit fails to meet the exigencies of some situation. Thus is evolved first an emotional consciousness and then within this, as we have already seen, an intellectual consciousness (in this case, conscious cognition) which defines and controls this emotion. From this standpoint feeling is just unanalyzed consciousness; it is total, vague, impulsive consciousness; hence the significance of the analysis of emotion into organic, kinaesthetic and dermal sensations.

(5) Initiative, attention, apperception, self-activity, are all traced back to elemental tendencies, instincts or tropisms, operating "at times when the results are not immediately adaptive." If the adaptation were perfectly smooth and unimpeded there would be no need for the evolution of such phenomena as attention and initiative. These are the product of, and are developed to meet the necessities of disadaptation in experience. The orderly control of experience in attention and direction of experience in so-called self-activity are the result of a selection from among a great number of still unadaptive movements

in which the animal persists despite their inefficiency. This is what Professor BALDWIN has called functional selection from excess movements or over-production of variations in the individual. Important questions arise at once to some of which an answer is given in chapter XIII. Why are these tropisms not immediately adaptive, and why do animals persist in making these non-adaptive movements? Why should such conscious processes as attention develop thus at the points of disadaptation in experience? What is the psychology of this disadaptation or break in the experience? And, even more important, the psychology of the reconstruction or readjustment after the break, by means of the conscious attention thus evolved. Professor ROYCE answers the first of these questions by saying that "this factor, this peculiar persistence, *belongs to the temperament of the animal*" (315). He, I suppose, would hasten to add that this is no real explanation, since "temperament" is something itself to be explained rather than the explanation of anything. Would it be in line with his own argument to suggest that the approximate reason is that the ordinary inhibitory effect of the regular routine of habitual acts is removed. The animal is, so to speak, reduced to a state of psychoplasm or impulse because of the ineffectiveness of the customary modes of activity. The restlessness and persistence in unadaptive movements represent simply the releasing of tendencies which are ordinarily inhibited. Relative freedom from ordinary restraints results in a relapse into a comparatively primitive state of unmediated impulse, until new restraints can be established, new habits built up. This gives us a hint, at the same time, as to the true nature of the break or disadaptation and a suggestion as to the law of the readjustment or reconstruction. Apart from some such interpretation, one is impelled constantly, throughout this whole discussion of initiative, to ask the old question, whether there is ever any absolutely novel element in experience, and, if not, how there can be any real progress.

(6) One's feeling, after reading this delightful book, is one of satisfaction in finding the emphasis thrown once again upon the unity and continuity of experience, after so much analysis and dissection in recent psychology, but with this, perhaps out of it, springs a desire that the author had carried out his organic view of experience a little further and shown us, not only that action is the natural consummation of feeling and thinking, but also how feeling and thinking first appear because of the interruption of action. It is just the full appreciation of the significance of this emergence of consciousness within action, as itself a phase of action—that consciousness not only leads over into action

but arises from and within action—that is most needed at the present time to put psychology into right relations with biology, on the one side, and with philosophy, on the other. With biology, because herein we find a category common to both sciences—the category of action, of adaptation, or adjustment and readjustment. With philosophy, for a similar reason, that in the process of the reconstruction of experience we see the true functional significance of the psychical. One of the best features of the book before us is its insistance on the social character of consciousness, and upon the psychical individual as the centre for the initiation of new and progressive phases of social life. "Certainly a general view of the place which beings with minds occupy in the physical world strongly suggests that their organisms may especially have significance as places for the initiation of more or less novel types of activity" (301). "Social inventiveness depends upon individualistic restlessness" (327).

A recent writer has said that "we ought to turn our views of human psychology upside down and study what is now casually referred to in a chapter on habit or on the development of the will, as the general psychological law, of which the commonly named processes are derivatives." This Professor ROYCE has done in a way that will prove instructive to psychologists as well as to teachers.

H. HEATH BAWDEN.

The Fore-Brain of the Bird.[1]

The bird presents in its brain as in other features of its organization more marked specialization than is to be found in any other class of vertebrates. The bird brain has been the subject of comparatively few researches and our knowledge of its structure and of the significance of its several parts has been meager. In the fore-brain, especially, great difficulties to a right understanding of its morphology and physiology have been presented by the unusual size of its basal ganglion and the apparent absence of a true pallium over a large part of the fore-brain. The homology of the several parts of the basal ganglion, the extent, structure, and the connections of the pallium and the functional significance of the several areas or nuclei are perplex-

[1] Untersuchungen über die vergleichende Anatomie des Gehirnes, von Dr. LUDWIG EDINGER in Frankfurt a. M. 5. Untersuchungen über das Vorderhirn der Vögel in Gemeinschaft mit Dr. A. WALLENBERG in Danzig und Dr. G. M. HOLMES in London. Mit sieben Tafeln und elf Textabbildungen. Sonderabd. aus d. *Abhdlgn. d. Senckenb. naturf. Gesellschaft*, Bd. XX, Heft IV.

ing questions to the solution of which Dr. EDINGER has applied himself during several years. The very satisfactory results published in this paper EDINGER attributes in large part to the coöperation of WALLENBERG and HOLMES, which made it possible to study a very wide range of material, representing all the chief types of birds, and to study the course of fiber tracts by the degeneration method. The attempt to describe the centers and fiber tracts in so complete a manner that they may be recognized in any group of birds, may be regarded as fairly successful.

The key to the interpretation of the bird fore-brain is found in its development. The fore-brain in the early embryo presents the typical arrangement: a thick ventral wall formed by the basal ganglion and an extensive pallium forming the roof of the wide ventricle. The basal ganglion, however, grows much more rapidly than the pallium and eventually obliterates a large part of the ventricle and fuses with the pallium over the greater part of the lateral and dorsal regions. The ventricle becomes reduced to a narrow medio-dorsal cleft connecting occipital and frontal horns, the latter extending into the olfactory lobe. The parts of the pallium thus fused with the basal ganglion have been overlooked or wrongly interpreted by previous authors. It is usually marked off from the basal ganglion by a layer of cells or by a layer of medullated fibers—the *Stabkranz*—and even where it is not so marked its structure and connections, as well as its developmental history, show that it is a true pallium.

In the basal ganglion the author has identified the epistriatum and the nucleus thaeniae and their fiber tracts, the relations being essentially the same as in the brain of reptiles. The remainder of the basal ganglion, which is very greatly enlarged as compared with that of any other vertebrate, consists of a ventro-median mesostriatum, a dorsal hyperstriatum, and a lateral ectostriatum. The ventro-anterior end of the mesostriatum is divided into two nuclei, a median lobus parolfactorius and a lateral nucleus basalis. Although there are great differences in the size and functional importance of these two nuclei and of other parts of the basal ganglion, the brains of all birds agree in the main features. The fibers from the pallium and the hyperstriatum form a medullated fiber layer, the lamina medullaris dorsalis, over the dorsal surface of the mesostriatum which corresponds to the capsula interna of mammals. The fibers then pass downward through the mesostriatum to form the brachia cerebri on its ventro-caudal surface. A true capsula interna is occasionally present (parrot). It is as yet

impossible to compare the parts of the basal ganglion of birds with the nuclei in the corpus striatum of mammals.

Only a few of the more important facts in the arrangement of the fiber tracts can be mentioned here. The olfactory apparatus is very poorly developed. Only a single tract of fibers connects the lobus olfactorius with the rest of the fore-brain and the destination of these fibers is not described. The nucleus thaeniae sends a bundle to the ganglion habenulae. This is joined by a bundle from the occipital cortex (tractus cortico-habenularis) and by one from the more anterior portion of the basal ganglion. This bundle, which is not commented upon by the author, suggests the anterior portion of the tractus olfacto-habenularis, as it has been described in fishes. No tract which can certainly be considered as fornix has been found. The greater number of fibers, both ascending and descending, connecting the fore-brain with the thalamus are related to the striatum and not to the pallium. Especially interesting is a tract from the sensory nucleus of the V nerve to the nucleus basalis of the mesostriatum and a corresponding descending tract of the oblongata and possibly to the cervical cord.

The most of the fiber bundles connecting the pallium with other divisions of the brain are mingled with those of the striatum and are ascending fibers from the thalamus and mid-brain. Almost the only large descending tract from the pallium is the tractus septo-mesencephalicus, from the medio-dorsal portion of the pallium to the dorsal part of the thalamus and the tectum opticum. Its function is unknown. A commissura pallii connects the medio-dorsal cortex of the two sides. A tract connects the occipital cortex with the mid-brain beneath the tectum opticum. This bundle corresponds to the cortical optic tract in mammals. The various portions of pallium are interconnected by shorter and longer associational fibers. These are least developed in the medio-dorsal cortex. Other important fiber tracts connect the nuclei of the fore-brain with one another. The anterior commissure appears to be purely a commissure between the two epistriata.

The experimental works of SCHRADER, GOLTZ, and KALISCHER on the functions of the bird fore-brain are reviewed, and the results extended by means of the new anatomical facts. The fore-brain is not essential to either sensory or motor activities but exercises a directive influence on both which raises them above the plain of simple automatism. Removal of the pallium alone does not cause the bird to starve, unless the striatum also is injured. A certain degree of localization of function is present in the fore-brain of various birds. The mesostriatum has an important relation to the act of eating, probably mediated

by the tracts connecting it with the nuclei of the V nerve in the oblongata. The occipital cortex is important for sight. The median portion of the dorsal cortex seems to be especially concerned in the innervation of the limbs.

The text of 84 quarto pages is accompanied by eleven text-figures and seven plates, five occupied by elegant colored figures representing WEIGERT sections and two presenting the results of degeneration experiments. The paper is one of the most important recent contributions to the morphology of the vertebrate brain.

J. B. JOHNSTON.

The Optic Chiasma and the Post-optic Commissure.

This subject has been treated in two papers by Dr. BURTON D. MYERS. In the first[1] the chiasma alone was studied by the degeneration method in the toad, cat, dog, rabbit, monkey, owl and snake, the toad receiving the most thorough treatment. In the toad certainly and probably in the owl and snake the decussation in the chiasma is total. In the dog, cat and monkey the decussation is unquestionably partial.

In the second paper[2] the same author makes a more thorough study of the relations in the rabbit, using the method of v. GUDDEN. The optic nerves and tracts do not begin to become medullated until twelve hours after birth; accordingly enucleations of the eye made during the first day will result in total failure of medullation of the corresponding optic nerve fibers and very clear pictures can be secured by the WEIGERT method, the animals having been killed at various intervals after the operation.

The experiments show conclusively that the chiasma of the rabbit is partial, though the uncrossed fibers are few in numher. The relation of the optic fibers to the post-optic or inferior commissure can be determined by reason of the fact that the optic nerves become medullated earlier than the commissure. Comparisons of series of different ages made after enucleation of both eyes with similar series made after the enucleation of one eye permits an accurate study of the relations of the optic tracts to the commissure. In brief, three such commissures are recognized:

[1] The Chiasma of the Toad (Bufo lentiginosus) and Some Other Vertebrates. *Zeits. f. Morph. u. Anthropologie*, III, 2, 1901.

[2] Beitrag zur Kenntniss des Chiasmas und der Commissuren am Boden des dritten Ventrikels. *Archiv f. Anat. u. Physiol.* Anat. Abt., 1902.

1. The commissura inferior of GUDDEN, or Commissura arcuata posterior of HANNOVER. . GUDDEN termed this the com. inferior in transverse sections, but the com. superior MEYNERTI in horizontal sections. Its fibers are closest to the chiasma at their crossing and go out laterally closely associated with the optic tracts.

2. The rostral part of the decussatio subthalamica anterior of GANSER. This is GUDDEN'S commissure of MEYNERT, and it may properly retain the name, MEYNERT'S commissure. Its crossing lies dorsally of the com. inferior, and its fibers also go out with the optic tracts laterally.

3. The caudal part of the decussatio subthalamica of GANSER. This may retain the name GANSER'S commissure. Its fibers after the crossing run back on each side of the body nearer the median line than either of the others and they envelop the fornix tracts laterally of the third ventricle.

The contradictory accounts of earlier authors are carefully reviewed in the light of the author's experimental results and it is to be hoped that the conclusions reached may set at rest the synonomy of this confusing region. It is needless to add that a real understanding of these commissures (or decussations, as they probably are) cannot be hoped for until we know the exact terminal relations of all the types of neurones involved.

There is described a curious mesial slip of the optic tract which runs up along the inner side of the inferior commissural tract. There is, the reviewer may add, an exactly similar detached portion of the optic tract in the bony fishes, which terminates in the nucleus geniculatus externus. C. J. H.

Peripheral Nerve Endings in Amphioxus.[1]

The description of the course and distribution of the sensory and motor nerves confirms in general the results of HEYMANS and VAN DER STRICHT. The most important part of the paper deals with the peripheral endings of the sensory nerves. Two sets of fibers are distinguished. The first pass through the homogeneous *Hautschicht* by means of special canals and reach a position immediately beneath the epithelial cells. Here they branch and form a subepithelial plexus from which "eine Menge feinster varicöser Fädchen" pass up and end between the epithelial cells, The second set of fibers have their cells

[1] Das periphere Nervensystem des Amphioxus (Branchiostoma lanceolatum). Von A. S. DOGIEL, St. Petersburg. *Anat. Heften*, Heft LXVI. p. 147-213, Pl. XII-XXIX. 1902.

of origin in the epithelium. These resemble the sense cells of invertebrates. Their outer ends reach to the surface but are not provided with sense hairs. Their inner ends are continued centrally as fibers which enter the sensory nerves. These sense cells are found generally in the epithelium and especially in the oral tentacles where they are grouped to form the special sense organs which have heretofore been compared with the taste buds and end buds of typical vertebrates. Nothing is stated with regard to the central relations of these two sets of fibers. The author describes certain structures which he regards as spinal ganglia but their finer structure is not sufficiently well made out to warrant any conclusion as to their character. J. B. J.

On the Lobus Impar of the Brain of Cyprinoid Fishes.[1]

In his work entitled, "Vom Bau des Wirbeltiergehirns," B. HALLER describes extensive anastomoses between nerve cells in the lobus impar of the medulla oblongata of the cyprinoid fishes and states that this structure is an especially favorable object for the demonstration of such anastomoses. GROTH examined haemalum, carmine and GOLGI preparations of several carp-like fishes in order to check up the observations of HALLER, but without finding any evidence of such anastomoses. There is an extensive but uncritical review of the literature of these brains and some description from his own preparations of the anatomical structure of this part of the brain, in the course of which, however, nothing of morphological importance is brought out.

C. J. H.

[1] GROTH, A. Ueber den Lobus impar der Medulla oblongata bei Cyprinoiden. Dissertation. *München*, 1900.

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